A STUDY OF A NAMURIAN CRUSTACEAN-BEARING SHALE FROM THE WESTERN MIDLAND VALLEY OF SCOTLAND

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Abstract

Crustaceans from a finely laminated shale above the Top Hosie Limestone (Limestone Coal Group) were discovered in 1981 by Mr S. P. Wood at Bearsden, near Glasgow. Spores common to the *Bellispores nitidus-Reticulatisporites carnosus* (NC) Zone, conodonts from the *Kladognathus-Gnathodus girtyi simplex* Zone, and goniatites of *Crave noceras leion* E1 Zone, suggest a Pendleian (Namurian) age for the shales. These shales form part of a newly defined formation, the Manse Burn Formation, for which the type locality is the Manse Burn, near Bearsden (NS529427329-NS53057325). The Manse Burn Formation has been further subdivided into six members on the basis of the fossil content and sedimentological characteristics of the shales, the Shrimp Member, the Posidonia Member, the Nodular Shale Member, the Platey Shale Member, the Betwixt Member, and the Lingula Member. The Shrimp Member of the Manse Burn Formation has been recognised at several other localities in the western Midland Valley of Scotland, the Hindog Glen (NS27905115), the Swinlees Glen (NS29415342), the Powgree Burn (NS33635219), Lochermill (NS24106472), the Red Cleugh Burn (NS65567846), the Burniebrae Burn (NS66037818), the Corrie Burn (NS68707876), and at East Kilbride (BGS bore hole data, filled quarries locations unknown).

The Shrimp Member, which contains the greatest abundance of crustaceans, is restricted to a basin bound to the north by the Paisley Ruck and the Campsie Fault, to the south by the Dusk Water Fault, to the west by Arran, and to the east by the Kincardine Basin and the central Glasgow Basin. The areas to the north, west, and south are considered to be areas of positive relief during the deposition of the Manse Burn Formation. To the east the basin was open to either marine or fresh water influences dependant on seasonal increases in the freshwater input. The shales of the Manse Burn Formation were deposited in conditions which varied in both oxygenation and salinity conditions. The Shrimp Member was deposited in an environment which was seasonally influenced by marine or non-marine water sequentially, the Posidonia Member and the Platey Shale Member were deposited in more marine episodes with variable oxygen levels, the Nodular Shale Member and the Betwixt Member

represent shales with the least marine character, and the Lingula Member has characteristics of both marine and non-marine influences and variable oxygenation levels. Towards the top of the Manse Burn Formation, the deposit becomes sandier with the onset of more terrestrial conditions. The Shales of the Manse Burn Formation appear to have been deposited in a low-energy back barrier lagoon with restricted marine access from the east.

Many of the crustaceans have been preserved in francolite, which has prevented the normally rapid bacterial decay of the crustaceans, preserving the helicoidal ultrastructural detail of the cuticle, and possibly a representation of the original chemistry as well. The sodium concentration of the cuticle may provide a key to the life environment and salinity tolerances of the crustaceans. The crustaceans are also preserved as drusy calcite outlines, and calcareous microconcretions. Other modes of preservation include the rosette calcite structure of the myodocopids, pyrite replacement of the bivalves and some crustaceans, and the calcite recrystallization of bivalve shells.

The crustaceans contained within these shales include, *Tyrannophontes pattoni*, *Tealliocaris robusta*, *Crangopsis eskdalensis*, *Palaemysis dunlopi*, *Minicaris brandi*, and *Cyclus rankini*. The first four of these, and *Cyclus rankini*, are members of the same palaeocommunity, which is here defined as the Western Midland Valley of Scotland Crustacean Palaeocommunity. *Minicaris brandi* is not considered to be part of the same palaeocommunity, as it is not preserved in the same manner as the other crustaceans, and is thought to have entered the back barrier lagoon from streams or rivers. *Tyrannophontes* is considered to be a stenohaline stomatopod adapted to normal marine conditions. *Tealliocaris* is a euryhaline decapod which appears to be best adapted to waters of higher salinity. *Crangopsis* and *Palaemysis* both appear to be euryhaline and adapted to cope with lower salinities as well as normal marine salinities. The distribution of the crustaceans in the back barrier lagoon suggests that the salinity decreases towards the west.

Pseudotealliocaris etheridgei is synonymised with *Tealliocaris etheridgii* and *Tealliocaris robusta*, and doubt is cast on the validity of the genus

Pseudotealliocaris. *Waterstonella grantonensis* is considered to be synonymous with *Crangopsis eskdalensis*, and specimens of the former differ only in their state of preservation. *Aratidecthes* is possibly synonymous with *Palaemysis*, based on a comparison of the published figures of *Aratidecthes* and the newly observed morphological characteristics of *Palaemysis*. *Cyclus rankini* is retained within the genus *Cyclus* due to the similarity of morphology and relative dimensions with the convex forms of this genus.

Enterospirae from the Shrimp Member provide an account of the interactions between the predators within the back barrier lagoon. One distended spiral heteropolar enterospire may represent a gut-fill of a *Petromyzon*-like animal. Most of the enterospirae are compact spiral heteropolar in form and contain abundant fish debris. Several enterospirae contain abundant bivalves and may represent gut-fills of an animal, which either lacks a stomach, or has an alkaline stomach, such as that found in chimeras.

Enterospirae can also provide useful information on the diagenetic pore fluids which pass through the shales as they contain a large amount of primary porosity. Fluids rich in calcite, quartz, and kaolinite, produced early cementation of the pores. A later baryte cement infills some enterospiral pore spaces. One enterospire from the Shrimp Member provided a $^{87}Sr/^{86}Sr$ ratio of 0.708 suggesting a marine source for the strontium. The $\partial^{13}C_{PDB}$ (-11.24, -11.29) and the $\partial^{18}O_{PDB}$ (-7.22, -7.32) values suggest, however, that the phosphatisation of the enterospire occurred in meteoric conditions.

Chapter 1

Introduction

This project was initially conceived as a result of a palaeontological excavation of Namurian (Lower Carboniferous) crustacean bearing shales carried out at a site in the Manse Burn, Bearsden, near Glasgow, from April 1981 to September 1982, by Mr. S. P. Wood, formerly of the Hunterian Museum (Glasgow University). The main aim of this project, as first formulated, was to determine the environmental and evolutionary significance of the crustaceans collected from this locality.

1.1 The Bearsden excavation.

A short history of the discovery, and excavation of the Bearsden locality, based on letters (*comm.*), notes (*not.*), radio and television interviews (*rad./TV interv.*), and press cuttings (*press cut.*) held in the files of the Hunterian Museum, is presented below.

1.1.1 The discovery of the crustacean bearing shales of the Manse Burn.
On Sunday the 22nd of March 1981, Mr. S. P. Wood was walking his dog along the Manse Burn, near his home in Bearsden, when he happened upon some fossiliferous shales (Wood 25 March 1981 *comm.*, Good Morning Scotland 2 July 1981 *rad. interv.*, Collier 1982). The Bearsden and Milngavie District Council were duly notified of the discovery (Rolfe 23 April 1981 *comm.*), and permission was soon granted for a small exploratory excavation to proceed (Rae 1 May 1981 *comm.*, Rolfe 5 May 1981 *comm.*).

The discovery was later released to the press with details of the pending excavation (Hunterian Museum 23 June 1981 *comm.*). The excavation took place from the 24th to the 31st of June 1981. The first fossil crustaceans to be uncovered were *Palaemysis* and *Cyclus*, which were described as 'this beautiful creature', and 'circular like a new penny' respectively by Mr. S. P. Wood in an

interview (Good Morning Scotland 2 July 1981 *rad. interv.*). Other animals discovered, at this time, included eighteen species of fish, of which five were sharks, and five crustacean genera; *Palaemysis*, *Tealliocaris*, *Minicaris*, *Crangopsis*, and *Cyclus* (Wood 12 August 1981 *comm.*).

Despite the obvious success of the excavation, the local residents of the Baljaffray Estate were concerned about several matters concerning the site (McCulloch 7 September 1981 *comm.*):

1) no notice of the excavation was given to the local residents,
2) the excavation was left uncovered and unlit at night,
3) the course of the Manse Burn could have been altered, and
4) the hole was not satisfactorily filled-in.

These points were taken into consideration before a second larger excavation took place.

1.1.2 The major excavation in the Manse Burn, Bearsden.

A further application was submitted for a larger excavation to take place downstream of the initial site, with the added request for permission to sell some of the material obtained, to cover costs (Rolfe 1 February 1982 *comm.*). Soon after Mr. Wood had presented a lecture to the Geological Society of Glasgow (11 February 1982) on the Bearsden discoveries, permission for all requests regarding the second excavation were granted by the Bearsden and Milngavie District Council (Rae 3 March 1982 *comm.*, Rae 23 March 1982 *comm.*, Rolfe 25 March 1982 *comm.*). The excavation commenced on the 5th of April 1982, and work continued until the 13th of September 1982. Much of the funding for equipment was provided by the Nature Conservancy Council, and the manpower was provided by funding by the Manpower Services Commission Youth Opportunity Programme.

The progress of the excavation was interfered with by children causing delay and concern over the safety of the excavation site (Baljaffray Residents Association Newsletter May 1982 *comm.*). The site was eventually rendered hazardous by flooding caused by vandalism, and the site had to be filled-in in

accordance with the prior agreement between the Hunterian Museum and the Bearsden and Milngavie District Council (Milngavie and Bearsden Herald 4 November 1983 *press cut.*, 11 November 1983 *press cut.*).

The excavation was not only of great scientific interest, but also became an educational public relations exercise, stimulating much interest amongst local children, and the media (Milngavie and Bearsden Herald 6 August 1982 *press cut.*, 12 November 1982 *press cut.*, 11 February 1983 *press cut.*, 4 November 1983 *press cut.*, 11 November 1983 *press cut.*, Sunday Mail 27 June 1982 *press cut.*), being reported as far away as Trinidad (Trinidad Herald 29 July 1982 *press cut.*). A British Broadcasting Corporation television program was also produced to mark the discovery: 'Stan, Stan the fossil man' (BBC *TV interv.*).

Despite the site being of historic interest, no move has yet been taken to erect a vandal-proof plaque commemorating this discovery, although this suggestion has been accepted by the Bearsden and Milngavie District Council (Rae 16 December 1982 *comm.*).

1.1.3 Scientific recording and the resulting research projects.

A large amount of information and many specimens were collected by field assistants, volunteers, and staff from the Hunterian Museum, during the course of the major excavation at Bearsden. A record of this material is held in the Hunterian Museum, some of it being used in this thesis, presented either in the appendix or in graphical form with the text.

During the major excavation of the Bearsden locality, applications were made to the Natural Environmental Research Council for projects on the fish fauna, and the crustacean fauna. The project on the fossil fish from Bearsden was proposed by Dr. A. L. Panchen of Newcastle University and research was carried out by Mr. M. Coates.

The project on the crustacean fauna was proposed by Dr. W. D. I. Rolfe and Dr. G. E. Farrow of Glasgow University. Mr. J. G. Sharp, formerly of Edinburgh University, initially accepted the project but, soon after found himself unable

to continue the research. The project was finally allowed to continue with another researcher to which post the present author was appointed in October 1985. By this time Dr. G. E. Farrow had already left the Department of Geology at Glasgow University, and Dr. W. D. I. Rolfe accepted a post at the Royal Museum of Scotland in Edinburgh after the completion of a year of research on the project. Despite this move, Dr. W. D. I. Rolfe kept an active interest in the development of the project, and has contributed much to its progress. Dr. C. J. Burton has supervised the field research phase and final development of the project, which has led to the discovery of further crustacean bearing shales, at the equivalent horizon to those found at Bearsden, within the bounds of the Midland Valley of Scotland.

1.1.4 List of news items and broadcasts referenced.

2 July 1981, 06:30. Archaeological goodies beneath Bearsden. serial 073039/PB. Good Morning Scotland.

27 June 1982. Shark find. Sunday Mail.

29 July 1982. Big catch of well preserved prehistoric fish off Glasgow. Trinidad Guardian.

6 August 1982. Kids 'dig' those fossils. Milngavie and Bearsden Herald.

12 November 1982. Council may get shark fossil. Milngavie and Bearsden Herald.

11 February 1983. Shark display. Milngavie and Bearsden Herald.

4 November 1983. Fossil man's remarks irk council. Milngavie and Bearsden Herald.

11 November 1983. Fossils site not to be open to public. Milngavie and Bearsden Herald.

1.2 Aims and development of the project.

Olson (1952, 1966) proposed that there existed a general persistence of community structure through time despite changes in the component taxa. Schram (1981a) suggested that several Palaeozoic crustacean assemblages could be recognised as palaeocommunities, and that Olson's theory could be applied

to construct crustacean community phylogenies. The material collected from the excavation at Bearsden provided an opportunity to test Schram's (1981a) community hypothesis, as crustaceans characteristic of both the brackish water and near-shore marine communities were found. This thesis was also intended to test the validity of a crustacean community phylogeny hypothesis by a detailed study of the crustaceans obtained from the Bearsden excavation, and from other Palaeozoic localities around the world. Prior to any discussion of community phylogeny, it was important to determine whether of the crustacean communities, proposed by Schram (1981a), were acceptable. The assemblage of crustaceans from Bearsden was, therefore, critically examined in terms of their preservation, taxonomy, palaeoecology, and life environment. The bulk of this thesis concentrates on constraining the life environment of the Carboniferous crustaceans from the western Midland Valley of Scotland to produce a foundation on which future studies on fossil crustaceans could be built, perhaps eventually resulting in a better understanding of crustacean community phylogenies.

The main aims of this thesis were adapted slightly from the original proposal to place more emphasis on:

1) discovering the stratigraphical position of the shrimp bearing shales in terms of bio- and lithostratigraphy. The stratigraphical position of the Bearsden locality was initially not precisely known, due to the lack of exposed lithostratigraphical markers, although, it was correctly placed at the horizon of the Top Hosie Limestone (Wood 1982) on the basis of the biostratigraphy,

2) determining the sedimentary environment and palaeo-geomorphology (i.e. geographical and oceanographical situation) of these shales, from further shrimp bearing shales at the same geological horizon. Fieldwork in the Midland Valley of Scotland was carried out to determine the full extent of the shrimp bearing shales, which resulted in several new localities being discovered,

3) studying the diagenesis of the shales and preservation potential of the crustaceans, as well as studying the processes resulting in their preservation. In the light of much recent palaeontological interest in

taphonomy and early diagenesis, the phosphatisation of these crustaceans provided an opportunity to add to the debate, as well as to further constrain the environmental conditions in which the crustaceans lived,

4) analysing the phylogenetic relationships of the fossil crustaceans in terms of their anatomy and taxonomy. Despite the volume of work on the taxonomy of Carboniferous fossil crustaceans, the identification of some taxa is suspect, often because of lack of evidence. The richness of the faunas herein described justified an attempt being made to rectify existing phylogenies,

5) discussing the feasibility of applying community, and community phylogeny, to the assemblage of crustaceans from these shales. As the shales containing the crustaceans persists for a period of at least 10,000 years, the assemblage is considered to be a part of a palaeocommunity dominated by crustaceans. The crustacean community cannot be considered in terms of community phylogeny, as it is not possible to regard the community holistically, and therefore cannot be reliably compared with communities from other periods,

6) determining the palaeoecological significance of their association. An environmental discussion is constructed on the basis of the distribution of the crustaceans, and changes in the crustacean community, across the Midland Valley of Scotland. Chemical analyses of the cuticle may provide further constraints on the environmental tolerances of these crustaceans, and may explain their distribution within the Midland Valley of Scotland.

Chapter 2

Stratigraphy

The shales of the Bearsden locality of Wood (1982) have been identified at several other localities within the bounds of the Midland Valley of Scotland (MVS) and have been placed in their lithostratigraphical and biostratigraphical contexts. Biostratigraphically, these shales, which occur above the Top Hosie Limestone (THL), and the shales below the THL, have yielded conodonts from the *Kladagnathus-Gnathodus girtyi simplex* Zone, spores of the NC Zone, and goniatites of the Pendleian E1 Zone of the Namurian Series. Lithostratigraphically, the shales belong to the Limestone Coal Group. These shales belong to the newly named Manse Burn Formation, which has been further subdivided into Members broadly corresponding to the 'beds' presented by Wood (1982). The Manse Burn Formation has been erected to include the shales from the top the Top Hosie Limestone Marine Band to the base of the first thick sandstone. The THL is thought to be close to, but above, the boundary between the Brigantian (Viséan) and the Pendleian (Namurian) Currie (1954).

2.1 Biostratigraphy.

2.1.1 Conodonts (see Plate 4.2e, f).

Some unidentified conodonts from beds 'B' (=Posidonia Member) and 'D' (=Platey Shale Member) were recorded by Wood (1982). Most of these are 'S' elements probably from assemblages belonging to *Cavusgnathus* and *Gnathodus*. Further conodont elements were obtained, by acetic acid etching and by paraffin saturation of the shales from the Posidonia Member at Bearsden. This has provided Pa elements (45 elements in 1.3kg of shale) of *Cavusgnathus naviculus* (Hinde), *Gnathodus girtyi* Hass (morphotype 'intermedius'), *Gnathodus girtyi* Hass (morphotype 'girtyi'), and *Gnathodus girtyi* Hass (morphotype unknown) (Dean *pers. comm.*,1987, Higgins 1975, 1984).

The range of the elements based on the zonation of Higgins (1975, 1984), suggests that this assemblage belongs to the *Kladognathus-Gnathodus girtyi simplex* Zone of the Pendleian Stage. Clarke (1961), recorded a number of 'Pa' conodont element genera from the THL horizon in Scotland which included *Cavusgnathus inflexus* and *Gnathodus clavatus* which have since been synonymised with *Cavusgnathus naviculus* and *Gnathodus girtyi* respectively (Higgins 1975). Craig (1954) recorded a similar conodont fauna from the shales below the THL near Kilsyth.

The lateral segregation of conodont faunas can be modeled on their distribution relative to a shore line in the Dinantian and Early Namurian (Dean 1987). The *Cavusgnathus* element bearing animal is thought to be nectobenthic and euryhaline, living in littoral inner shelf waters. The *Gnathodus* element bearing animal, however, is thought to be a more offshore pelagic animal characteristically found in basinal environments of normal salinity. The distribution of *Gnathodus* appears to be governed mainly by ocean currents and temperature irrespective of bottom water conditions. The most likely environment present during the deposition of the Posidonia Member and the Platey Shale Member is that of a shallow shelf sea with normal marine salinity.

The conodont elements are found scattered over the bedding surfaces and have not been found in natural assemblage associations. This is presumably due to being moved by bottom water currents after decay of the soft body parts. In some specimens several Sc elements are found in close association, one is found as a partially disarticulated bedding-plane assemblage with one Pa element and some S elements.

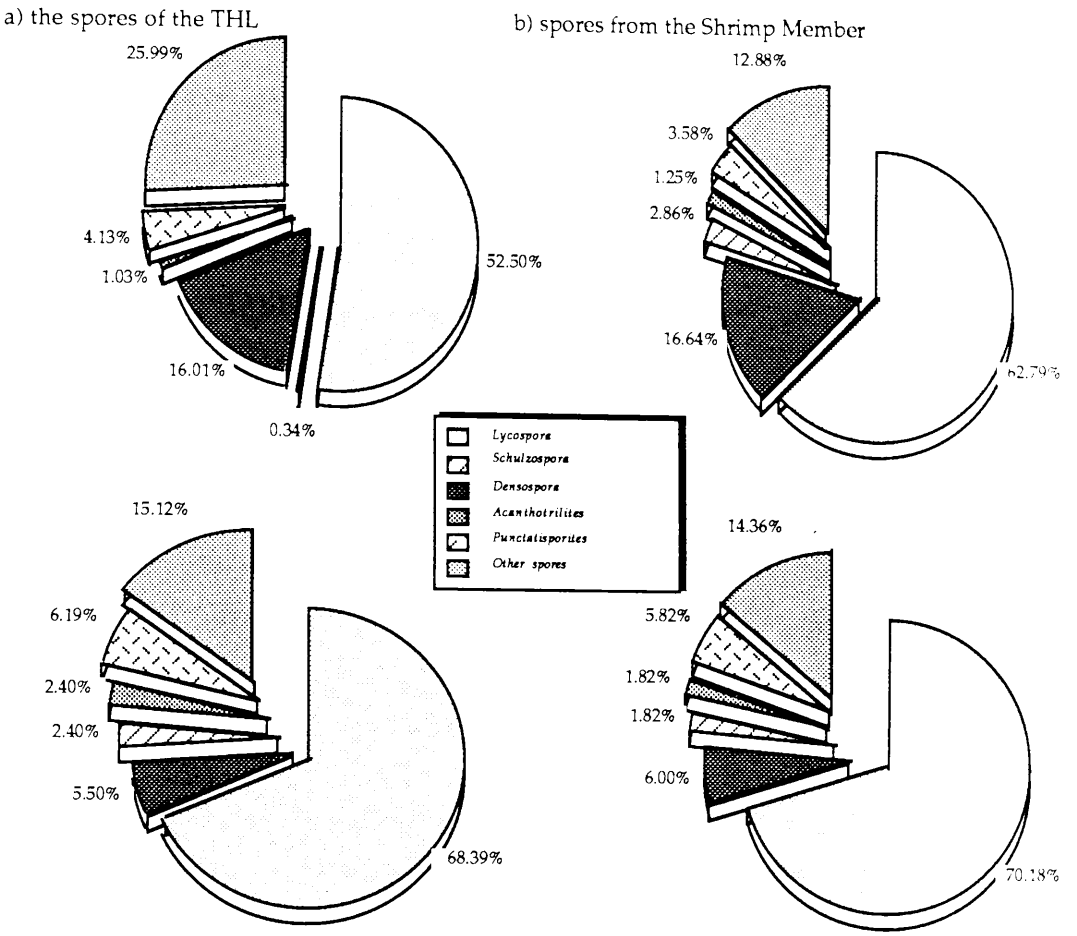
2.1.2 Spores (see Plate 4.2h, i, j).

The shales of the Shrimp Member to the Lingula Member at Bearsden, and equivalent localities near Glasgow, contain spore genera common to the *Bellispores nitidus-Reticulatisporites carnosus* (NC) Zone of Neves *et al.* (1972) (=*Rotaspora knoxi* (III) of Smith and Butterworth 1967). The lower

boundary of this zone was placed in the middle of the P2 goniatite zone (Brigantian) and extends to the top of the E1 goniatite zone (Namurian) (Owens *et al.* 1977). The most common of the spores are *Lycospora noctuina* Butterworth and Williams 1958, *L. pusilla* (Ibrahim) Schopf, Wilson, and Bentall 1944, *Densosporites annulatus* (Loose) Smith and Butterworth 1967, *D. intermedius* Butterworth and Williams 1958, *D. triangularis* Kosanke 1950, *Schulzospora elongata* Hoffmeister, Staplin, and Malloy 1955, and *Leiotriletes tumidus* Butterworth and Willams 1958. At the base of the Namurian E1 several new elements enter into the an expanded fauna (Owens *et al.* 1977). Elements of this expanded fauna are found at Bearsden including *Verrucosisporites morulatus* (Knox) Smith and Butterworth 1967, and *Grumisisporites rufus* (Butterworth and Williams) Smith and Butterworth 1967. *Bellispores nitidus* (Horst) Sullivan 1968 also occurs as a minor element at Bearsden.

Marine shale assemblages have different relative proportions of the various genera to those of coal-seams. The coal-seam assemblages are dominated by *Lycospora, Densosporites* and *Schulzospora,* and marine shale assemblages are dominated by saccate spores (Neves 1961). In non-marine shales there is a wider diversity of spore species containing both marine shale forms and coal seam forms due to intermixing of the microfloras. At Bearsden, the spores suggest a mixture of both a coal assemblage, dominated by *Lycospora, Schulzospora,* and *Densospora,* as well as a marine shale assemblage with *Acanthotriletes*. The THL, the Shrimp Member, the Posidonia Member, and a 5cm thick black mud from the Nodular Shale Member all have similar spore concentrations though a slight increase in the percentage of *Lycospora* can be observed up-succession suggesting a gradual increase in non-marine influences {500 spores were counted for each member and the THL) (Fig 2.1 a-d).

Figure 2.1 The spore composition of the Manse Burn Formation and the THL.



Correlation across the MVS is difficult due to the facies dependancy of the spores. Most spore studies have been based on coal seam assemblages to provide consistency in the analyses. The result of studies done across the Viséan-Namurian boundary show that their are no major microfloral changes (Butterworth 1967).

2.1.3 Goniatites.

Specimens of goniatites from the MVS are rare from the THL horizon and only a few well preserved goniatites have been previously recorded. The THL equivalent at East Kilbride has yielded *Crave noceras scoticum* Currie 1954 which has been compared with *C. leion* Bisat 1930 of the E1 index zone in England (Currie 1954) and is thought to represent an index fossil for the

Pendleian E1 of Scotland. Fragments of *C. scoticum* were found from shales below the THL horizon, along with fragments of *Dimorphoceras sp.*, placing the boundary between the Brigantian P2 (Viséan) and the Pendleian E1 (Namurian) stages below the THL (Currie 1954). The specimens of *Dimorphoceras*, also found at East Kilbride, are similar in form to *D. plicatilis* Moore 1939 (Currie 1954).

2.1.4 General comment.

Aisenverg *et al.* (1979a) suggested that the Pendleian may correspond to the Lower Serpukhovian of the Lower Carboniferous in the USSR. The upper limit of the Lower Carboniferous in the USSR is taken to be the boundary between the Serpukhovian (Namurian E1-H2 goniatite zones) and the Bashkirian (Namurian R1 goniatite zone-Lower *similis-pulchra* non-marine bivalve zone of the Westphalian B) where there is a major extinction (Aisenverg *et al.* 1979a, 1979b). In Britain, until recently, the boundary between the Lower and Upper Carboniferous has been taken to be at the base of the Namurian E1 (Higgins 1984). It is now thought to occur at the major extinction at the top of the Upper *muricatus* Zone at the top of Arnsbergian (=goniatite zone E2 of the Namurian) (Lane and Manger 1985; Ziegler and Lane 1987) which is equivalent to the Mississippian-Pennsylvanian boundary in North America (Aisenverg *et al.* 1979b), but below the extinction recognised in the Russian stratigraphy of the Donetz Basin (ie: the Serpukhovian (Namurian H2)-Bashkirian (Namurian R1) extinction).

Although many of the species used in the biostratigraphic zoning of this part of the Carboniferous are long ranging, the associations of species suggest that the shales of the Manse Burn Formation belong to the basal Pendleian (Namurian, Lower Carboniferous).

2.2 Lithostratigraphy.

2.2.1 Sedimentation and stratigraphy of the Lower Carboniferous in the MVS.

The Carboniferous of the MVS consists of sediments of laterally varying

thickness which lie, for the most part, conformably on Old Red Sandstone sediments. The Tournaisian, the Viséan, and the basal part of the Namurian (Francis 1983; Aisenverg *et al.* 1979a, 1979b) form the three stage subdivision of the Lower Carboniferous. The Middle Carboniferous is also well represented in Scotland, from the middle Namurian to the upper Westphalian (Aisenverg *et al.* 1979a, 1979b).

The Tournaisian lithologies are mainly argillaceous and dolomitic limestones of a semi-arid environment. These gave rise in the early Viséan to oil shales in an enclosed basin surrounded by the Clyde and Forth lavas to the north, west and east and by the Southern Uplands to the south, with alluvial sedimentation periodically invading the basin from the NE, in Fife.

Shallow marine limestones interfinger with the deltaic sandstones and coals in later Viséan times becoming more fluvio-deltaic in the early Namurian. Marine conditions produced limestone sequences in the later Namurian, of the Middle Carboniferous, which gave rise to a further shallowing and the deposition of fluvial sediments with only the occasional marine incursion. In the Westphalian, fluvial sedimentation continued with the addition of coal-bearing strata.

Table 2.1 The Carboniferous succession in the Midland Valley of Scotland (after Patterson and Hall 1986, and Francis 1983).

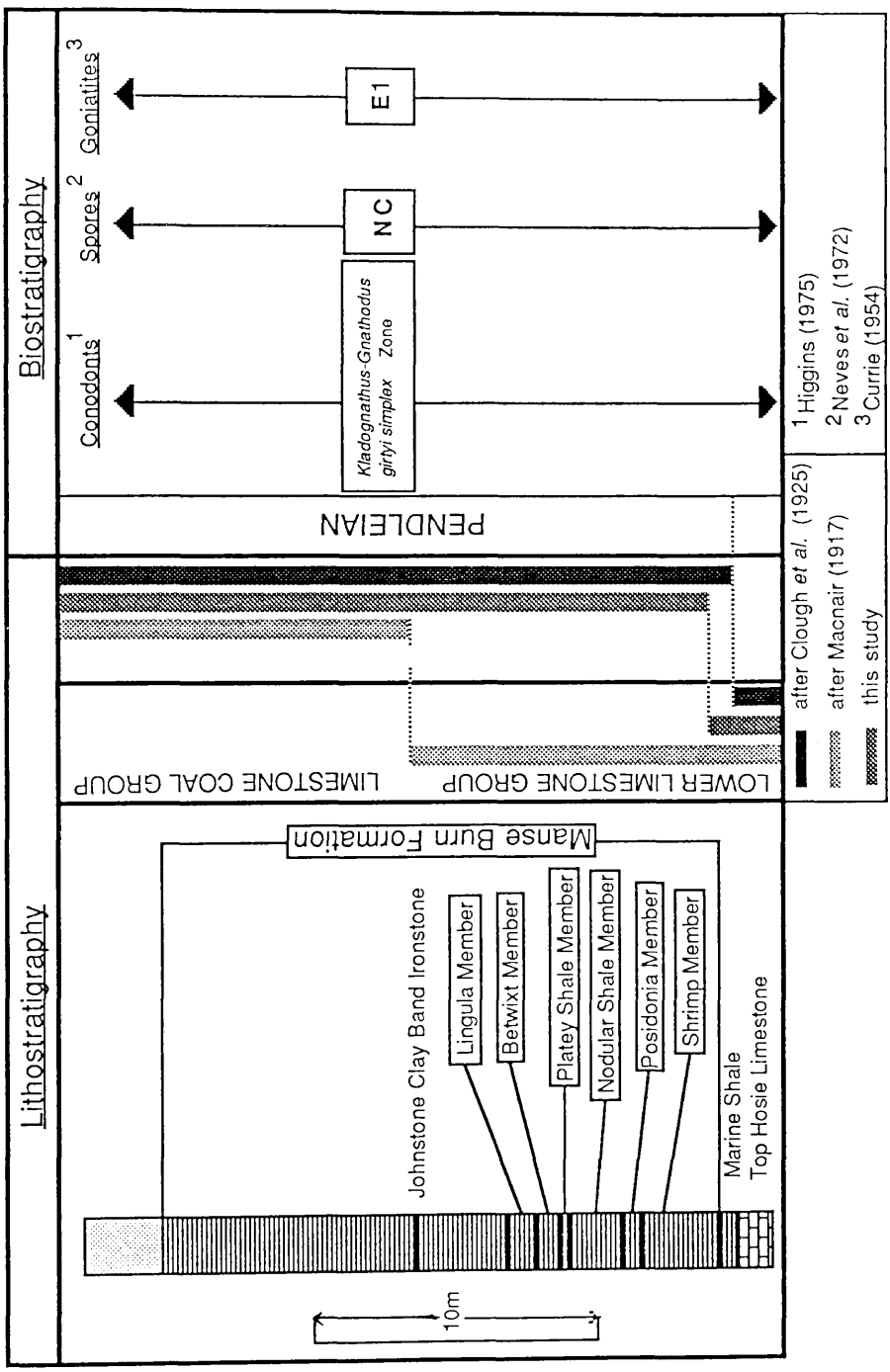
<table>
<tr><th>GROUP</th><th>FORMATIONS</th><th>AGE</th><th>Miospore Zone</th><th>Goniatite Zone</th></tr>
<tr><td rowspan="2">LIMESTONE COAL GROUP</td><td></td><td rowspan="2">LOWER CARBONIFEROUS (NAMURIAN)</td><td rowspan="2">NC</td><td rowspan="2">E1</td></tr>
<tr><td>Manse Burn Formation</td></tr>
<tr><td>LOWER LIMESTONE GROUP</td><td></td><td rowspan="5">LOWER CARBONIFEROUS
(DINANTIAN)</td><td rowspan="2">VF</td><td>P2</td></tr>
<tr><td rowspan="2">STRATHCLYDE GROUP</td><td>Lawmuir Formation</td><td rowspan="3">↑</td><td rowspan="3">P1
↑</td></tr>
<tr><td>Clyde Plateau Volcanic Formation</td></tr>
<tr><td rowspan="3">INVERCLYDE GROUP</td><td>Clyde Sandstone Formation</td></tr>
<tr><td>Ballagan Formation</td><td rowspan="2">CM</td><td rowspan="2">B1</td></tr>
<tr><td>Kinnesswood Formation</td><td>UPPER DEVONIAN</td></tr>
</table>

The correlation of chronostratigraphic units across the MVS is based mainly on

the correlation of laterally extensive lithologies and formations (George *et al.* 1976). The lowest lithostratigraphic unit, the Calciferous Sandstone Measures, has recently been revised and subdivided into two groups; the Inverclyde Group and the Strathclyde Group. The Inverclyde Group includes part of the Upper Old Red Sandstone from the old nomenclature (Paterson and Hall 1986). The actual boundary between the Upper Devonian and the Lower Carboniferous is, however, still unclear due to a lack of zone fossil evidence.

Above the Calciferous Sandstone Measures in the MVS is the Lower Limestone Group which is bounded at the base by the Hurlet Limestone and at the top by the THL. The Limestone Coal Group overlies the Lower Limestone Group and includes the Manse Burn Formation at its base in the Glasgow area (see Tables 2.1, 2.2). The boundary between the Brigantian and the Pendleian corresponds closely with the boundary between the Lower Limestone Group and the Limestone Coal Group (Francis 1983).

Table 2.2 The Biostratigraphy and Lithostratigraphy of the Manse Burn Formation.



2.2.2 The Manse Burn Formation.

The Manse Burn Formation, and its associated members, are defined according to the stratigraphical procedure suggested by Holland *et al.* (1978).

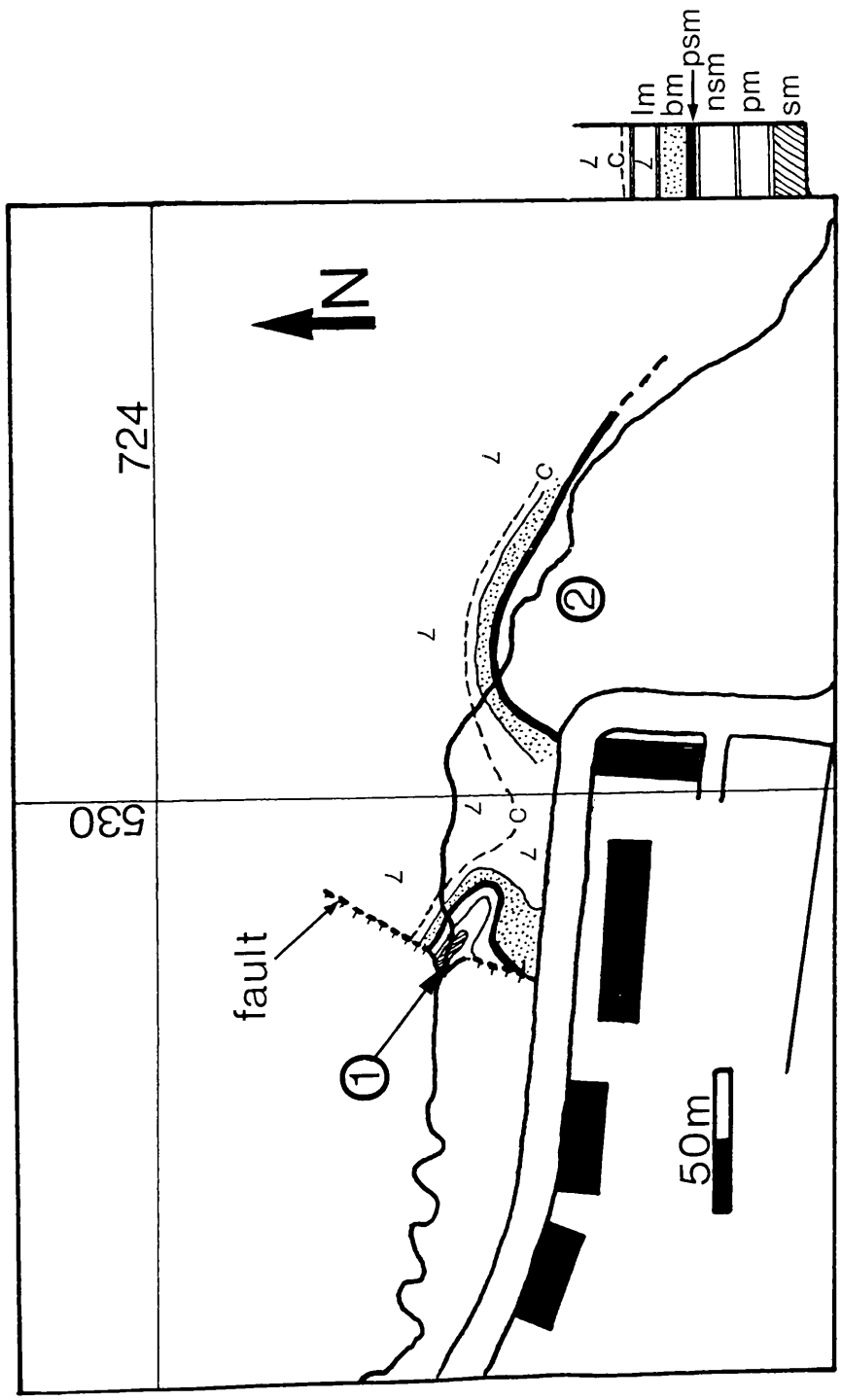
Type locality: Manse Burn, Bearsden, Strathclyde Region, NS52947329-NS53057325 (Ordnance Survey sheet NS 57 SW)

Boundaries: The upper boundary of the Manse Burn Formation is not exposed at this locality but is represented at other localities by a thick unnamed sandstone unit. The lower boundary is the upper limit of the Lower Limestone Group which is represented by a marine shale containing a similar high diversity fauna to the THL. The formation consists mainly of dark grey shales containing a restricted fauna. The faunal changes resulting from minor changes in environmental conditions delineate further divisions, or members, within the Manse Burn Formation.

Description: The Manse Burn Formation consists mainly of shales although it also includes the Johnstone Clay Band Ironstone. The formation is here further subdivided into six members reading from the base upwards, the Shrimp Member, the Posidonia Member, the Nodular Shale Member, the Platey Shale Member, the Betwixt Member, and the Lingula Member.

The Shrimp Member is not fully exposed in this area and its full extent was not realised during the excavation of Wood (1982). It is faulted against the marine shale at the top of the Lower Limestone Group at the northwestern exposure (NS52947329). The sediment at this horizon is a grey shale consisting of fine laminae and a fauna consisting mainly of crustaceans, fish, and bivalve spat. This member is called the Shrimp Member due to the large number of crustaceans obtained from this horizon during the excavation (Wood 1982). It can be as much as 280cm thick in the Burniebrae Burn of the Campsie Hills.

Figure 2.2 Locality map for the Manse Burn at Bearsden, near Glasgow, 1=position of initial excavation; 2=position of major excavation; sm=Shrimp Member; pm=Posidonia Member; nsm=Nodular Shale Member; psm=Platey Shale Member; bm=Betwixt Member; lm=Lingula Member; c=*Crangopsis* marker band; grid lines are NS724 and NS530. This map is based on a map held by the NCC Geological Review Unit, Newbury, and by the Hunterian Museum (Wood 1982).



The Posidonia Member is well exposed and consists of 48cm of dark fissile shale containing abundant *Posidonia corrugata*. The fauna also includes other bivalves, nautiloids, goniatites, *Euphemites sp.*, juvenile gastropods, bivalve spat, *Productus sp.*, plant debris, conodonts, fish, and sharks. This member can be traced to other localities in the Campsie Hills and is reported to contain specimens of *P. corrugata* of up to 15cm breadth (Macnair and Conacher 1914). Rare eumalacostracan crustaceans have been reported from the top of this member (Wood 1982).

The Nodular Shale Member is also well exposed at Bearsden and is largely devoid of macrofossils except for the occasional bivalve and very rare crustaceans. The shale is poorly bedded and contains a number of calcareous nodules of about18cm width and 7cm height and also three thin mud beds (1cm, 1.5cm, and 5cm thick). The total thickness of this member is approximately 187cm.

The Platey Shale Member is approximately 28cm thick and consists of a dark grey fissile shale containing rare disarticulated fish debris and abundant bivalve spat. The fauna also includes other bivalves, conodonts, nautiloids, and rare eumalacostracan crustaceans and *Lingula*.

The Betwixt Member is largely unfossiliferous but occasionally contains solitary bivalves and ostracods. It consists approximately 80cm of poorly bedded grey shales and is called the Betwixt Member because it separates the more marine shales of the Shrimp Member through to the Platey Shale Member from the less marine shales of the Lingula Member.

The Lingula Member consists of a number of interbedded calcareous shales with poorly fissile shales which contains a fauna of *Lingula* and *Naiadites* along with rare eumalacostracan crustaceans. A 0.2cm *Crangopsis* marker band occurs at the base of this member (Wood 1982). The thickness of the Lingula Member is not fully exposed at this locality but is over 100cm thick. Conodonts have been found associated with *Crangopsis* in the marker band.

The rest of the Manse Burn Formation is not exposed at this locality and has not been subdivided further as most of the rest of the formation is unfossiliferous except for the Johnstone Clay Band Ironstone. None of the micaceous shales and siltstones which occur above the Lingula Member, and below the thick mature sandstone which tops the formation in the Campsie Hills, are exposed at the Manse Burn locality. The total thickness of the Manse Burn Formation in the Campsie Hills is approximately 40m.

The Manse Burn locality was chosen as the type section for the Manse Burn Formation because most of the fossiliferous members are presently exposed, there is easy access to the exposures, and the locality was the site of a major excavation conducted by the Hunterian Museum. The only problems with this locality are that the base of the Shrimp Member, and part of the Lingula Member, and above, are not exposed here.

2.2.3 The distribution of the Top Hosie Limestone.

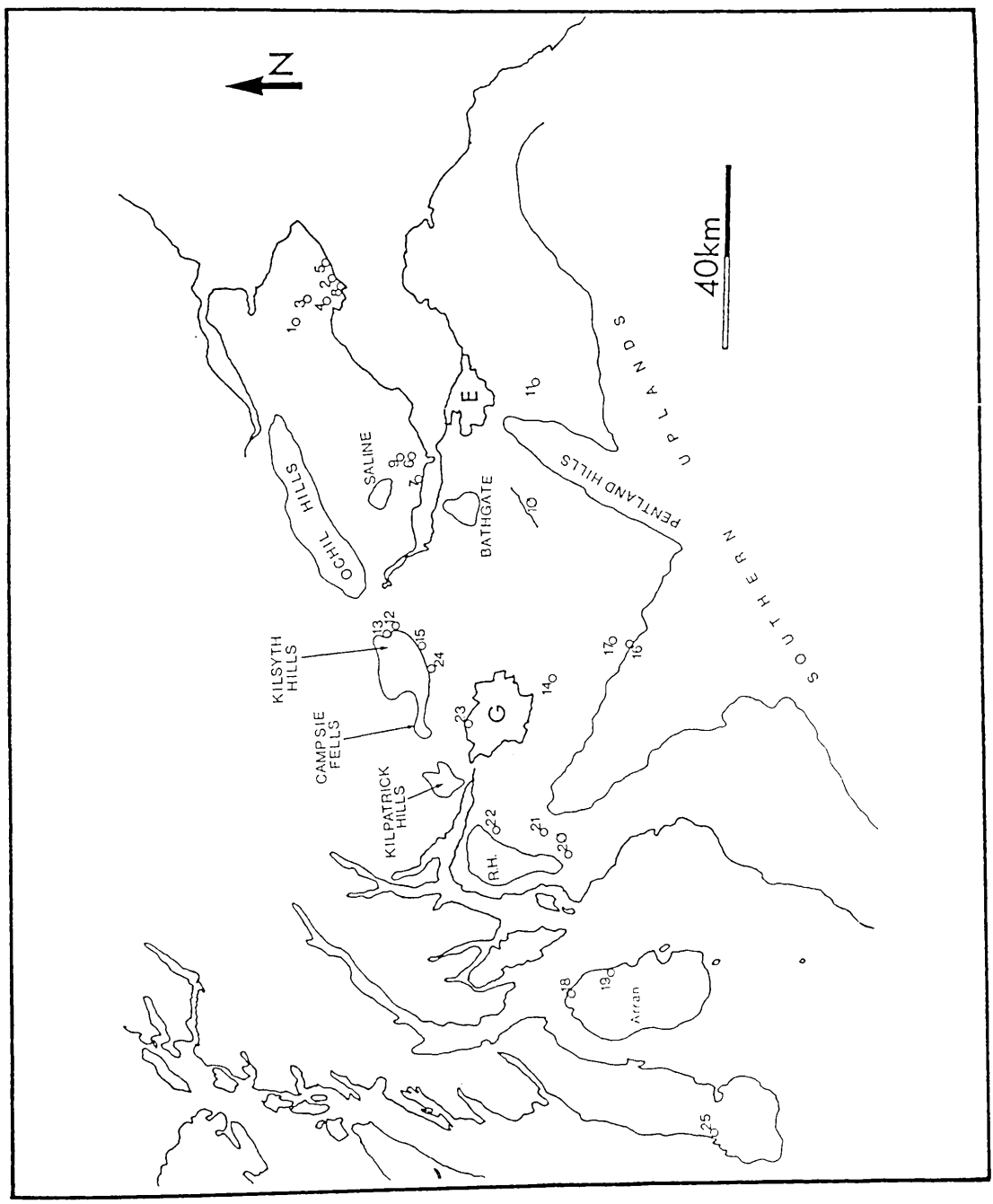
The distribution of the THL was studied to determine the lateral extent of the members within the Manse Burn Formation and to assess the shrimp-bearing potential of the shales overlying the THL to provide constraints on the distribution of the Shrimp Member.

The THL has been much documented in the past and has been shown to extend laterally across most of the MVS and has been correlated with other limestones and marine shales based on their palaeontology and relative position within the stratigraphic column. It is especially prominent and best exposed in the Glasgow area. The top of the THL has been taken to represent the top of the Lower Limestone Group of the Carboniferous Limestone Series (Clough *et al.* 1925; Whyte 1981; Forsyth and Wilson 1965; Wilson 1966; Mykura *et al.* 1967). Macnair (1915, 1917) extended the Lower Limestone Group to include the Johnstone Shell Bed (Table 2.2) and Clough *et al.* (1925, p46) suggested that an equally good argument could be made for placing the boundary between the Lower Limestone Group and the Limestone Coal Group at the even higher level of the Black Metals. The position of the boundary between the Lower Limestone Group

and the Limestone Coal Group is taken, herein, to be the top of the marine shale containing a highly diverse benthic marine fauna similar to that contained in the THL. The position of the boundary between the biostratigraphic zones of the Brigantian P2 and the Pendleian E1 goniatite zones, however, occurs somewhere below the Top Hosie Limestone. This should not be confused with the position of the boundary between the Lower Limestone Group and the Limestone Coal Group which is based on lithostratigraphic units.

In East Lothian, the limestone at the top of the Lower Limestone Group is the Barness East Limestone of Barness (Peach and Horne 1910). Closer to Edinburgh there are few exposures of the equivalent horizon. In the Bilston Burn there is a good section of the Lower Limestone Group including the Bilston Burn Limestone which is considered to be the equivalent of the THL (Peach et al. 1910). The Bilston Burn Limestone is equivalent to the Limestone no. 3 of Howell and Geikie (1861).

Figure 2.3 Locality map for the Midland Valley of Scotland. 1=Ceres; 2=Ardross; 3=Radernie; 4=Lathallan; 5=St. Monans; 6=Balbougie; 7=Charleston; 8=Elie; 9=Cowdenbeath; 10=Briechwater; 11=Bilston Burn; 12=Denny; 13=Dunipace; 14=East Kilbride; 15=Corrie Burn; 16=Muirkirk; 17=Lesmahagow; 18=Laggan; 19=Corrie; 20=Dalry; 21=Beith; 22=Bridge of Weir; 23=Bearsden; 24=Spouthead; 25=Machrihanish; R.H.=Renfrew Hills; G=Glasgow; E=Edinburgh.



In Fife, the THL horizon is also not very well exposed. The top of the Lower Limestone Group here is thought to be the Upper Kinniny Limestone. In eastern Fife this level is represented by a marine shale, the lower limit of which has been taken to be the upper limit of the Lower Limestone Group by Forsyth *et al.* (1977). The maximum thickness seems to be confined between the Ardross and Ceres faults in the Lathallan-Radernie zone (Forsyth *et al.* 1977). The Upper Kinniny is found in the stream below Balbougie near Inverkeithing and is recognised by the abundance of *Bellerophon* (Peach et al. 1910). *P. corrugata* has been recorded from the Upper Kinniny Limestone horizon near Charlestown and Rosyth in a shale below the limestone (Peach et al. 1910). On the shore at Elie there is an exposure of the Red Limestone (Cummings 1928) which has been identified as being equivalent to the THL (Forsyth et al. 1977).

In the Bathgate area (West Lothian) of West Kirkton and Petershill, the equivalent horizon to the THL is taken up by lava flows. In the area north of Bathgate the basalts occupy the thickness between the Wardlaw Limestone and the Index Limestone and to the south the lavas diminish, although they are still present at Blackburn (Geikie *et al.* 1879).

Towards Denny and the Campsie Hills in the northern area of the Carboniferous outcrop of the MVS the exposure of the THL improves. In the River Carron the Hosies are represented by a few thin limestones amongst thick sandstones and shales. The Hosies have been quarried further north where they become thicker, at Northfield and Quarter (Howell and Geikie 1861). In the Cumbernauld and Kilsyth District the THL is exposed in the Corrie Burn, near Queenzieburn, where it is overlain by the Posidonia Member (Howell and Geikie 1861). Further to the west near Milton of Campsie the THL is exposed with the Posidonia Member in the easterly branch of the Spouthead Burn, and also in the Burniebrae Burn (Howell and Geikie 1861).

In the Renfrew District the THL is poorly exposed but has been worked at Lochermill near Bridge of Weir. The shales above the THL are poorly exposed at Lochermill (Carruthers and Richey 1915, Macnair 1915) but show

similarities in the faunal content to the shales further east. The Hosie 'D' is thought to represent the THL in Ayrshire due to the presence of *P. corrugata* shales below the limestone (Richey et al. 1930, Clough et al. 1925, Wilson 1979).The exposures in the Pitcon Burn and the Hindog Glen do not contain the Posidonia Member but do contain crustaceans from the Shrimp Member. The THL is well exposed in the Dusk Water near Beith (Richey *et al.* 1930).

In Arran the Hosies are exposed in the Laggan section to the north of the island where the total thickness of the Lower Limestone Group is considerably thicker than in the southern exposures at Corrie and near Brodick Castle (Gunn et al. 1903). The strata between the Corrie Limestone (=Hurlet Limestone) and the Index Limestone consists mainly of thick sandstones and flags with the occasional shale (Gunn et al. 1903).

In central Ayrshire the THL is represented by an iron cementstone overlain by a hard sandy shale, the McDonald Coal and the Johnstone Shell Bed within a thickness of 1.76m in the Wyndy Burn near Nethershield (Eyles *et al.* 1949). To the SE of the Kerse Loch Fault the sediments of the Lower Limestone Group become considerably thicker and there are more and thicker limestones and coals (Richey 1937; Eyles *et al.* 1949; Goodlet 1957). In the Patna and Dalmellington area the exposures are not very useful, however, bores indicate that the Patna Limestone is overlain by the Doon Limestone which is considered to be the equivalent of the upper Hosie (Eyles *et al.* 1949). Further south at Dailly, the THL is well exposed but the Posidonia Member is not found here. Several bores north (Raithill, Whitehill, Southcraig and Mossbog) and south (Houldsworth and Glaisnock) of the Kerse Water Fault as well as some natural exposures at Sorn (north), and Muirkirk, New Cumnock, Waterside and Dailly (south) show the thickening of the sediments of the LLG is of the order of three to four times (Eyles *et al.* 1949).

In the Muirkirk District the THL is represented by the McDonald Limestone which can be over 10m thick (Geikie *et al.* 1873). An unusually thick Hosie 'D' is exposed in the streams beween Galston and Kilmarnock (Richey et al. 1930). The Douglas Water of the Clydesdale District contains similar sections of the

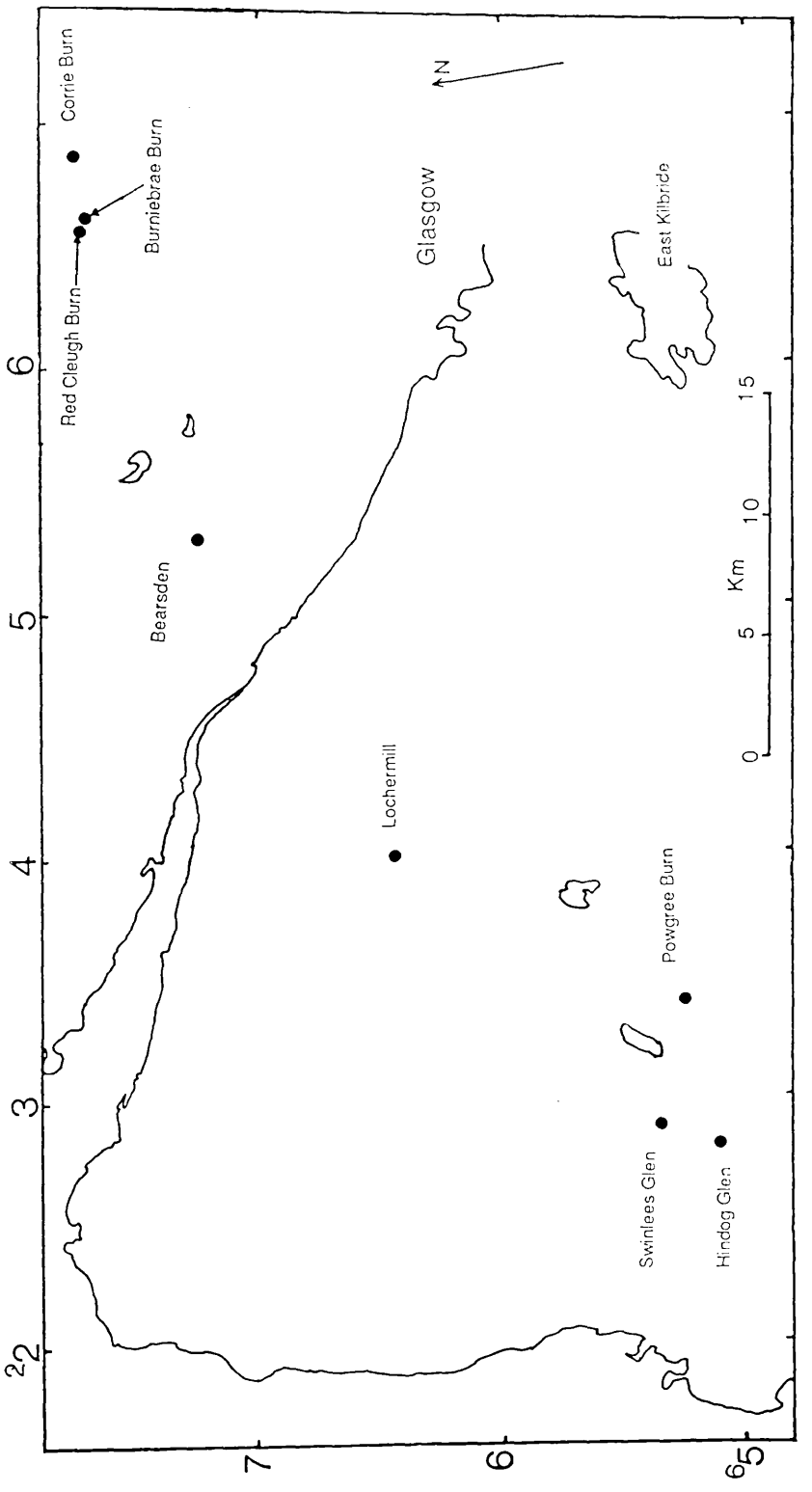
McDonald Limestone despite a rapid attenuation from the west to east (Geikie *et al.* 1871). The Moss Burn, Penbreck, Wildshaw and Whitecleugh outliers have a well developed Lower Limestone Group with the McDonald Limestone similar to that of Muirkirk (Geikie *et al.* 1871).

The Hosie 'D' is exposed at Lugton and Meikle Cutstraw near Stewarton but nothing is known of the overlying beds (Richey *et al.* 1930). Further to the east at East Kilbride the Calderwood Cementstone represents the uppermost limestone of the Lower Limestone Group and is exposed at a number of localities (Macnair 1917). *P. corrugata* is present above and below the Calderwood Cementstone allowing a correlation with the THL to be made (Macnair and Conacher 1914). To the NE, at Carluke, the THL has been recognised from bore holes. The calmy limestone from this area, exposed in Jock's Burn and Fiddler's Gill, occurs above the 1st Kingshaw Limestone and probably represents the THL (Geikie *et al.* 1879).

2.2.4 The distribution of the Shrimp Member of the Manse Burn Formation.

The bulk of the project is based on the fauna preserved within the Shrimp Member. It is, therefore, necessary to discuss the distribution of this member to provide a more complete picture of the sedimentological constraints on the environmental and ecological conditions affecting the fauna. During the period of this study, several previously unrecorded localities for the Shrimp Member were discovered in the Burnie Brae Burn, the Corrie Burn, Hindog Glen, the Powgree Burn, and Swinlees Glen. Lochermill was only known from museum collections, and many of the localities around East Kilbride are from bore hole data from the British Geological Survey. The old quarry exposures at East Kilbride which provided crustaceans in the past are now all filled in. Bearsden and the Red Cleugh Burn were the only two localities still exposed which had been previously recorded as having a crustacean fauna (Schram 1979, Wood 1982).

Figure 2.4 Locality map for the Shrimp Member of the Manse Burn formation.



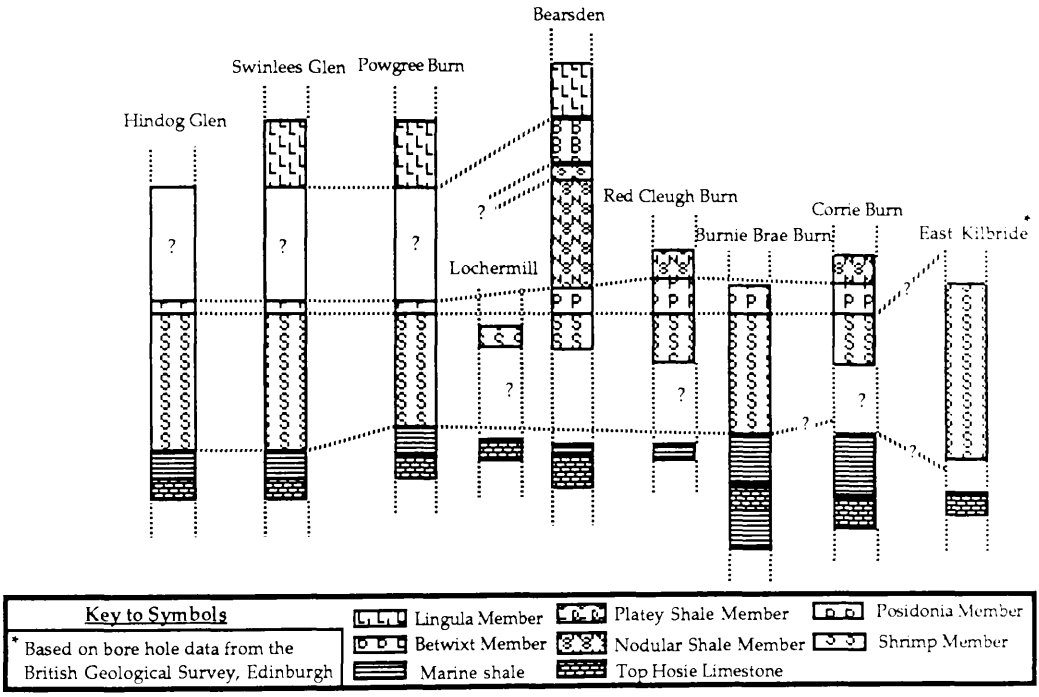
The most easily recognised member of the Manse Burn Formation is that of the Posidonia Member due to the great abundance of the bivalve *Posidonia corrugata* in a characteristically dark fissile shale. Wilson (1966, p126) noted that *P. corrugata* ranged from the Bollandian (P1) to the Arnsbergian (E2) and occurred most abundantly in the shales above the THL. The distribution of shales containing abundant *P. corrugata* in the Glasgow area has been discussed by Macnair and Conacher (1914) and Macnair (1917). At many of these localities it is possible to find the Shrimp Member or at least evidence that the Shrimp Member was exposed in the past (Carruthers and Richey 1915). The first record of crustaceans from the shales above the THL was that of Patton and Coutts (1885, p327) who recorded *Palaemysis*, *Palaeocrangon* (=*Crangopsis*), *Palaeosquilla pattoni* (=*Tyrannophontes pattoni*), and *Anthrapalaemon couttsii* (=*Tealliocaris robusta*) from East Kilbride, and Neilson (1895, p71) also recorded the existence of *Anthrapalaemon* and *Dithyrocaris*. At East Kilbride *P. corrugata* was found to be present above and below the THL, and the crustaceans are identical in preservation to those collected from the Shrimp Member elsewhere. Most of the crustaceans from this area were later described in detail by Peach (1908). Although the East Kilbride localities are now lost, several bores by the British Geological Survey in this area have provided specimens of *Crangopsis* from the Shrimp Member at various levels above the THL (see Table 3.2).

The Shrimp Member and the Posidonia Member are exposed in the Corrie Burn (NS68707876), near Queenzieburn, in the easterly branch of the Spouthead Burn (the Red Cleugh Burn, NS65567846), and the Burniebrae Burn (NS66037818), near Kilsyth, where the presence of *P. corrugata* above the THL was recognised by Howell and Geikie (1861). The crustaceans, and other elements of the fauna, are most abundant at these localities.

At Lochermill near Bridge of Weir (NS24106472), the shales above the THL are poorly exposed but contain the same faunal elements and preservation as the Shrimp Member. The Swinlees Glen (NS29415342), the Hindog Glen (NS27905115), and the Powgree Burn (NS33635219), near Dalry have the Shrimp Member exposed above the THL but with much fewer crustaceans. The

Posidonia Member at these localities does not appear to contain *Posidonia corrugata*, but does contain abundant bivalves (*?Ctenodonta*). The overlying member appears similar in character to both the Nodular Shale Member and the Betwixt Member and the Platey Shale Member was not observed. The diversity and distribution of the crustaceans is discussed further in Chapter 6.

Figure 2.5 Correlation of the Manse Burn Formation based on localities at which the Shrimp Member was present.



2.3 Correlation with Ireland.

The Carboniferous basin of NW Ireland is bounded by the Moinian and Dalradian metamorphics of Donegal to the north and the Longford-Down Ordovician to Silurian massif to the south. The basin consists of a number of NE-SW trending synclines separated by anticlines of Precambrian to Lower

Devonian rocks (Higgs 1984). Based on biostratigraphical data, the boundary between the Brigantian and the Pendleian of this area has been placed between the Carraun Shale Formation and the Dergvone Shale Formation (Brandon and Hodson 1984; Higgs 1984). The Carraun Shale Formation is represented by basinal or prodelta to turbidite or delta front deposits near the top which extends into the lower Dergvone Shale Formation. The Camderry Member of the Carraun Shale Formation commonly contains *P. corrugata* and the base of the Gubaveeny Shale Member contains abundant bivalves and goniatites as well as phosphatic nodules. *P. corrugata* and *Pseudamusium praetenuis* are common in the *Eumorphoceras medusa* beds of the Gubaveeny Shale Member (Brandon and Hodson 1984). The Dergvone Shale Formation is at the equivalent stratigraphical position as the Manse Burn Formation and appears to represent an environment more exposed to open marine conditions.

Further to the east into northern Ireland near Ballycastle, the trend of the syncline of Carboniferous rocks is ENE-WSW (Bishopp et al. 1948). This Main Limestone of this basin has been correlated with the Hurlet Limestone of the MVS and the McGildowney's Marine Band with the Index Limestone (Wilson and Robbie 1966). The Main Limestone and the Main Coal represent the upper beds of the Brigantian and the intervening lithologies are mainly micaceous and calcareous sandstones with some fossiliferous shales and coals. *Lingula* occurs in the more marine beds (Wilson and Robbie 1966). The sediments of the Ballycastle area have been correlated with the Carboniferous lithologies of Machrihanish (Macallien and Anderson 1930; Wilson and Robbie 1966). The rocks of Machrihanish represent more terrestrial conditions with only a few fossiliferous limestones. Macallien and Anderson (1930) suggested the existence a Highland Border Ridge which separated the sedimentary basins of the Machrihanish-Ballycastle from the MVS. This would result in the restricted marine conditions in the northwestern MVS, which is supported by the paucity of genera represented in the Manse Burn Formation.

The Carboniferous to the south between Loughshinny and Naul, near Dublin, has Brigantian (P2) overlain directly by Namurian (E2) (Bishopp *et al.* 1948). This does not mean that deposition did not occur but may rather indicate a

period of erosion which removed the sediments of the basal Pendleian during the later Pendleian, or early Arnsbergian.

Direct lithostratigraphic correlation of Scotland and Ireland has been made between Machrihanish and Ballycastle, the sediments further west may represent more distal deposits of a large interconnected series of smaller sedimentary basins extending as far as Fife. The western Irish section may represent the source direction from which the intermittant marine transgressions occurred, which can be observed in the western MVS.

Chapter 3

Sedimentology

The Midland Valley of Scotland was situated near the equator in what was probably a hot, humid climate during the deposition of the sediments of the Lower Limestone Group and Limestone Coal Group (Read 1988). Some of the sediment was derived from the south, and from the islands within the valley (Mykura *et al.* 1967), but most of the sediment came from the north to northeast (Read 1965; Read and Dean 1967, 1976, 1982). There was an opening to the marine waters to the west, and possibly to the east as well, from Brigantian times into the Namurian (Goodlet 1957; Mykura *et al.* 1967).

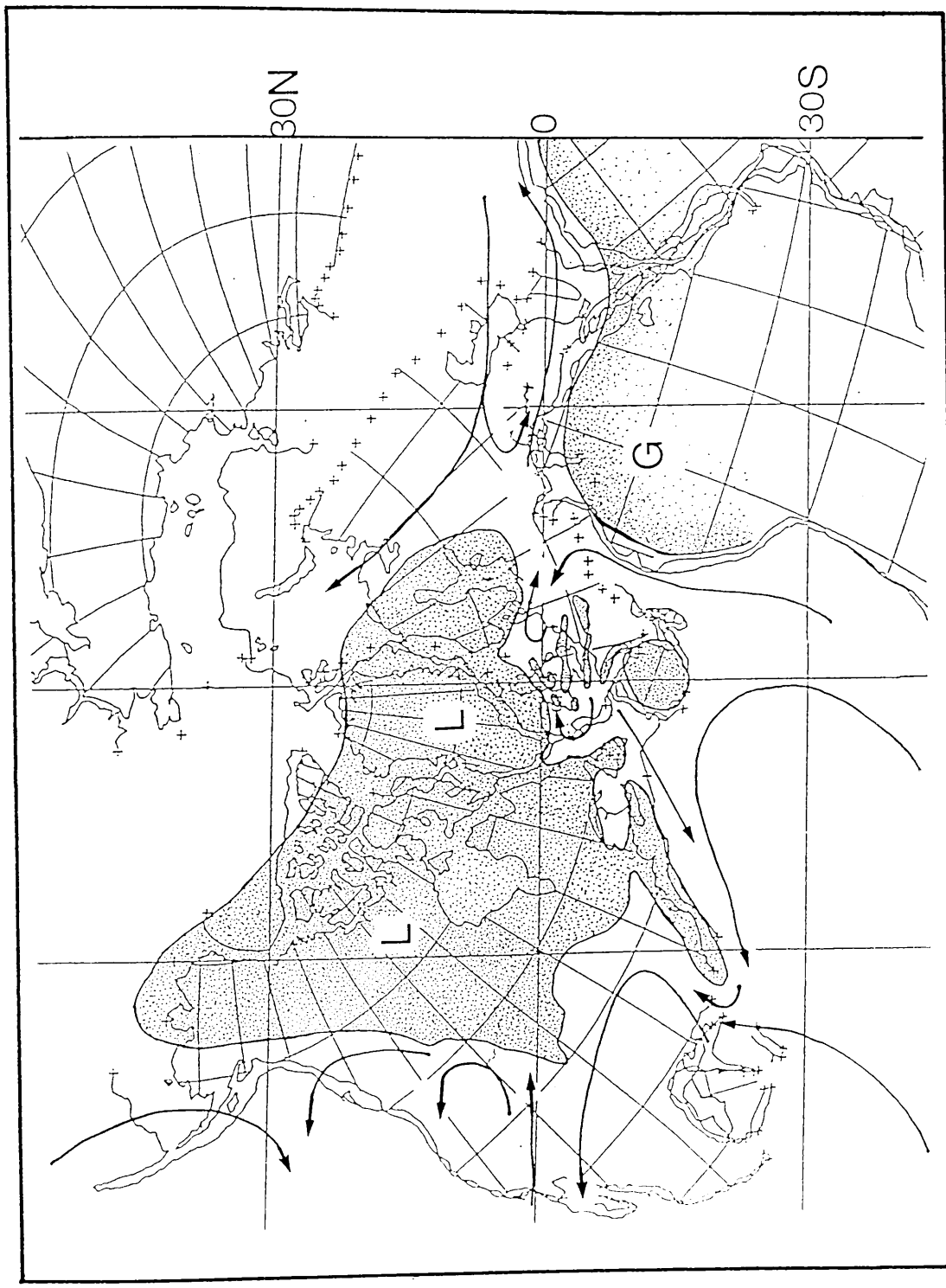
The lithostratigraphy of the Carboniferous of the Midland Valley of Scotland is based on its laterally extensive limestones, coals and sandstones. The extent of these lithologies depended greatly on the geomorphology of the Carboniferous landscape at the time of deposition, whereas the rates of deposition and sediment types depended on the tectonic environment and the aqueous environment. The chemistry of the sediments is governed by the source rocks, the diagenetic pore fluids, the environmental conditions, and biogenic activity. In this chapter the palaeogeography, chemistry, and petrography of the shales of the Manse Burn Formation are discussed, together with the tectonic controls on sedimentation, to provide a model of the depositional environment.

3.1 Geological setting for sedimentation in the Midland Valley of Scotland during the Lower Carboniferous.

3.1 1 Palaeogeography.

There are three recognised continents existing during the Namurian; Laurasia, Gondwana, and eastern Eurasia (Smith *et al.*, 1981). Their distribution is established mainly on palaeomagnetic and sedimentological evidence for latitude and palaeontological evidence for longitude (Smith *et al.*, 1973, 1981). Eurasia west of the Urals, Iberia, Greenland, and North America constitute the

Figure 3.1 Palaeogeographical map showing the continental distribution and possible surface currents during the Namurian (based on Smith *et al.* 1981 and Dewey 1985). L=Laurasia; G=Gondwana (land masses are stippled).



Laurasian continent which extended from about 20° south to 30° north of the palaeoequator (Dewey 1985, Van der Zwan *et al* 1985). Although there are a few inconsistencies in the palaeomagnetic evidence, such as data obtained for Newfoundland which suggests that it was 20° south of the palaeoequator (Irving and Strong 1984), the overall picture is that the southern margin of Laurasia straddled the equator during the Carboniferous (Smith *et al* 1973, 1981, Dewey 1985, Van der Zwan *et al* 1985) (Fig. 3.1). The Midland Valley of Scotland is on the southeastern edge of this continent within a few degrees of the palaeoequator and derives the majority of its sediment from that continent (Goodlet 1957; George 1958; Francis *et al.* 1970, Read 1988).

The islands which are thought to occur along the southeastern margin of Laurasia are drawn on the reconstruction which is based on a combination of the reconstructions by Smith *et al.*(1981) and Dewey (1985). The positioning of Gondwana and eastern Eurasia is arbitrary as they do not appear to affect the sedimentation in the Midland Valley of Scotland, although a dextral strike slip movement is thought to occur between them suggesting that they were quite close (Badhham 1982, Dewey 1985). Their relative position, during the Devonian and Carboniferous, would have affected the marine surface currents, which in turn affected the crustacean biogeography.

The earliest benthic eumalacostracan *Palaeopalaemon*, which is not found beyond the Devonian rocks of eastern North America, may have had a restricted eastward dispersal due to northerly current directions along the western coastline of the Laurasian continent (Schram *et al.* 1978, Dewey 1985, Hannibal and Feldmann 1985). Other eumalacostracans which are common to the Viséan and older rocks of Pennsylvania (Schram 1988) and southern Scotland (Schram 1979) indicate widespread dispersal at an early stage in the evolutionary development of these crustaceans (Schram 1977). The poor preservation potential of the malacostracan crustaceans is a major controlling factor in the distribution of localities, which tend to occur within ≈10° of the palaeoequator (Dewey 1985, Hannibal and Feldmann 1985), the reason being that the equatorial region developed the early diagenetic conditions necessary for the preservation of the crustaceans, by phosphatisation or concretion

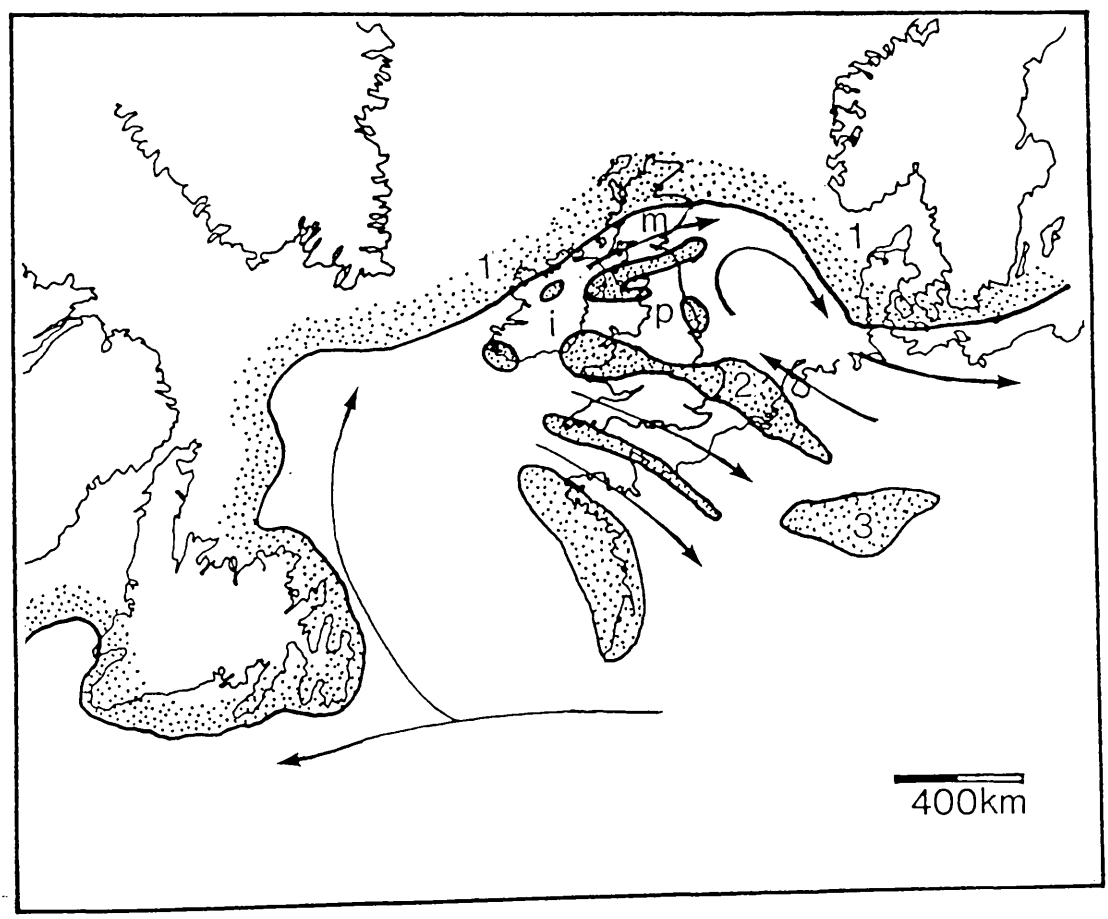
generation (see Chapter 4). The resulting inadequacy of the fossil record, with respect to the crustaceans, prevents the recognition of a centre of dispersal. Despite the difficulty in identifying this centre of dispersal, it is thought that the initial dispersal came from the east, due to the presence of abundant early Carboniferous crustacean faunas in Scotland and from the hypothetical westerly flow directions of the equatorial surface ocean currents at that time (Abele 1982, Dewey 1985).

The later crustacean faunas of the Namurian are found from the Midland Valley of Scotland of eastern Laurasia to the Bear Gulch deposits of central Montana, USA in western Laurasia. The fauna found in the Midland Valley of Scotland, at this time, is similar to that found in Montana, although there are more genera represented in the latter (Factor and Feldmann 1985, Schram 1979, 1981a, Schram and Horner 1978). It is possible that the crustaceans dispersed around the southern-most tip of Laurasia from east to west quite rapidly by the transport of planktonic larval stages in the westerly surface water currents(Dewey 1985). As some of the genera which co-occur at these localities have benthic morphologies, *Tealliocaris* (=*Pseudotealliocaris*), and palaeostomatopods, their rapid dispersal during the Lower Carboniferous is best explained by accepting the existence of a planktonic larval stage, although the fossil evidence may also be an artifact of their poor preservation potential.

The best known of the Lower Carboniferous crustacean localities of the south-eastern coast of Laurasia are those of the Northumberland Trough and the Midland Valley of Scotland (Schram 1979). These localities were positioned on, or very close to, the palaeoequator, and contain diverse crustacean faunas depending on the prevailing environmental conditions, controlled by such factors as salinity (see Chapters 4 and 6). This area, now represented by the British Isles, Ireland, and northwest Europe, was mostly submerged within a shallow, shelf sea embayment bounded by the Laurasian continent to the north, east, and southwest (Stainer 1916, Dewey 1985). Within this embayment were several major islands which restricted the flow of ocean currents allowing the more restricted and opportunistic faunas to develop. The power of the

surface currents affecting the Midland Valley of Scotland, where the Namurian Manse Burn Formation fauna is developed, is restricted in the south by the Southern Uplands Massif, by smaller islands within the bounds of the Midland Valley, and by the geography of Scandinavia, from the effect of open ocean currents from the Uralian Ocean (Goodlet 1957, Dewey 1985) (Fig. 3.2).

Figure 3.2 Palaeogeographical map of the British Isles during the Namurian (based on Dewey 1985), m=Midland Valley Basins; p=Pennine Basins; i=Irish Shelf; 1=Laurasia; 2=Wales/Brabant Massif; 3=Central Germany.

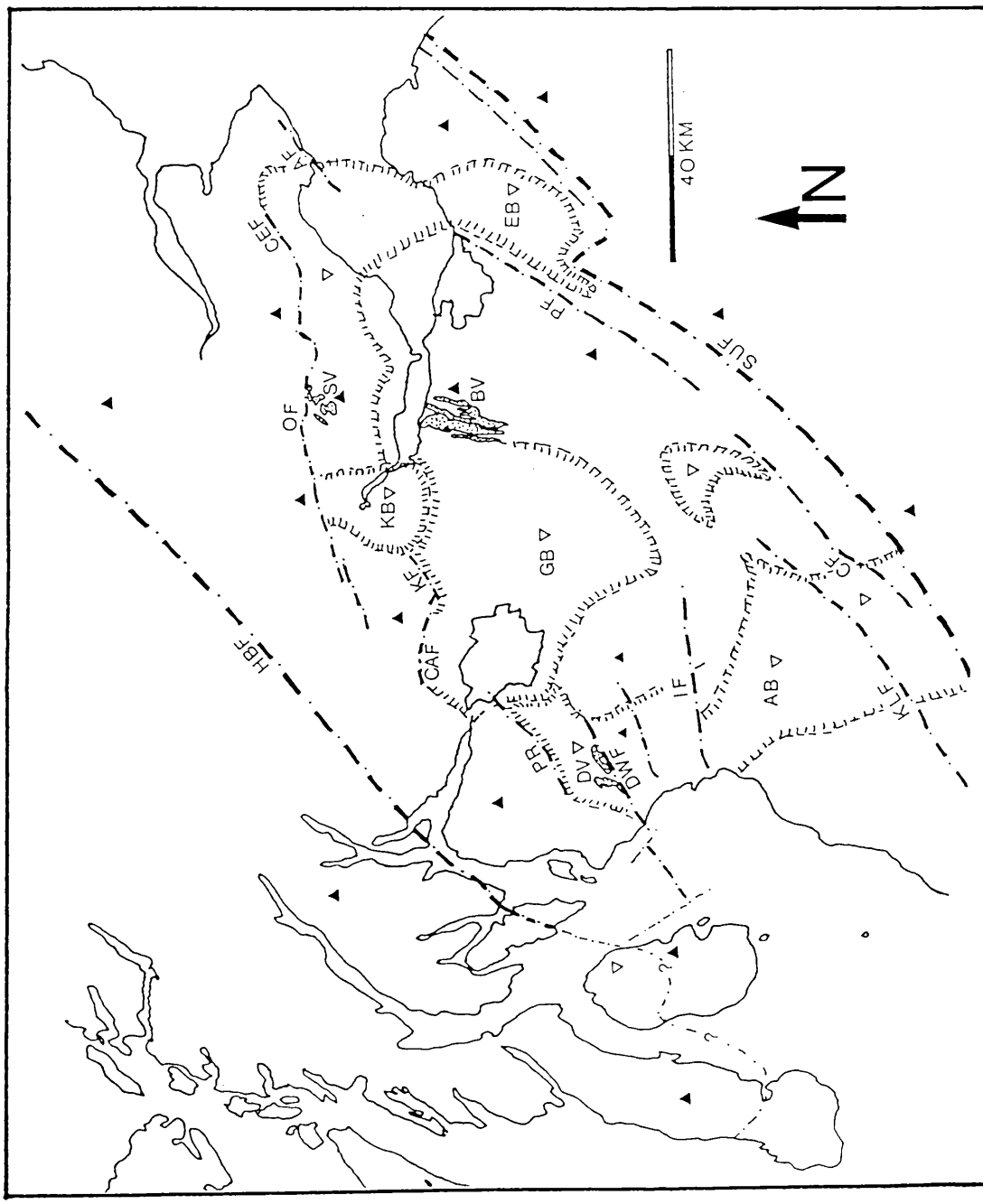


3.1.2 Structural controls on sedimentation within the Midland Valley of Scotland.

Sediment thickness in the Midland Valley of Scotland is governed by both isostatic and fault related subsidence which creates both widespread and local areas of greater sediment thickness (Goodlet 1957; George 1958; Francis *et al.* 1970). In the eastern MVS there is a general increase in the sediment thickness into Fife. In the central MVS, the Kincardine Basin and the Glasgow Basin are also marked by greater thicknesses of clastic sediments. The different thicknesses of sediments within the MVS are controlled by the syndepositional faulting resulting in local areas of positive and negative relief (McLean and Deegan 1978; Simpson and MacGregor 1932; Eyles *et al.* 1949; Goodlet 1957) (Fig. 3.3).

In the western MVS, in the Ayrshire shelf area, it appears that the sedimentation is controlled by subsidence along major syndepositional NE-SW trending faults during Lower Limestone Group times (McLean and Deegan 1978). These faults resulted in an increase of up to three times the thickness of the Lower Limestone Group sediments, across the Kerse Loch Fault towards the south. It was thought that this increased thickness continued as far as the Southern Uplands Fault (Simpson and MacGregor 1932; Eyles *et al.* 1949; Goodlet 1957). The other NE-SW trending faults, the Dusk Water Fault and the Inchgotrick Fault, are also thought to have affected sedimentation at this time, north and south of which, respectively, the thickness of sediments is much increased (Richey 1937). An area of relatively positive relief is, therefore, developed between these two faults. The Dusk Water Fault appears to have also been an important feature during the eruption of the Clyde Plateau Lavas (Alomari 1980), and seems to have produced a barrier to sedimentation during the deposition of the shales of the Manse Burn Formation, thick shales to the north and absent to the south. The sediments of the Manse Burn Formation are confined to the area north of the barrier produced between the Dusk Water Fault and the Inchgotrick Fault.

Figure 3.3 Map showing the geological structure of the Midland Valley of Scotland. AB=Ayrshire Basin; AF=Ardross Fault; Bathgate Volcanics; CAF=Campsie Fault; CEF=Ceres Fault; CF=Carmichael Fault; DV=Dalry Volcanics; DWF=DuskWater Fault; EB=Midlothian Basin; GB=Glasgow Basin; HBF=Highland Boundary Fault; IF=Inchgotrick Fault; KLF=Kerse Loch Fault; KF=Kilsyth Fault; KB=Kincardine Basin; OF=Ochil Fault; PR=Paisley Ruck; PF=Pentland Fault; SV=Saline Volcanics; SUF=Southern Uplands Fault; Syndepositional basins=open triangles; areas of little or no subsidence during the deposition of the Manse Burn Formation=closed triangles.



Towards the north of the MVS, the Dalradian block is thought to have been uplifted against the Highland Boundary Fault during the Upper Old Red Sandstone and formed an erosional surface at that time. Most of the Carboniferous rocks, however, appear to cross the Highland Boundary Fault with little regard to its presence, probably as a result of peneplanation (Bluck 1984).

The Campsie fault, which bounds the Manse Burn Formation to the north, is thought to have been more important than the Highland Boundary Fault in the controlling of sediment thickness in the Glasgow area. The Kincardine basin marks the eastern most development of the Shrimp Member of the Manse Burn Formation, probably as a result of an increase in fluvial conditions and clastic sedimentation from the north.

Towards the east, the area of maximum thickness in east Fife appears to be bound by the Ardross and Ceres faults in the Lathallan-Rademie zone (Forsyth *et al.* 1977). East Fife lay in an area of complex and variable subsidence allowing large amounts of clastics to be deposited (Forsyth *et al.* 1977). The sediments of the Manse Burn Formation are not developed in this area, although the Top Hosie Limestone is thought to be represented. The extent to which the Top Hosie Limestone occurs across the MVS suggests that it was the result of a widespread transgression, rather than being controlled by the syndepositional faulting within the MVS.

The process which resulted in the formation and distribution of basins and highs in the MVS has been much disputed. An understanding of the mechanisms is fundamental to any interpretation of the fault distribution and controls on sedimentation. The complex and variable subsidence within the MVS has been interpreted by three important models of the possible regional stress regime (Read 1988). The first of these is an E-W tension and the second a N-S tension both resulting in pure shear. The third is caused by early Devonian lithospheric stretching and crustal rifting followed by thermal subsidence with right-lateral strike slip (Dewey 1982). Stedman (1988) suggested that the almost N-S orientation of the areas of high and low subsidence in the northeast

of the Midland Valley of Scotland may be due to an E-W tensional regime associated with the onset of North Atlantic rifting. In the southwest, however, the depositional areas trend NE-SW which may be due to a heterogeneous basement (Bluck 1984) and reactivation of pre-existing structural trends (Stedman 1988) rather than being directly related to the stress regime present during the Lower Carboniferous. Stedman (1988) suggests a sinistral movement to explain the possible EW tensional regime.

A series of N-S trending Silesian folds, curving towards the NE in the north of the Midland Valley of Scotland and to the SW in the south, would suggest that dextral fault movement on the Highland Boundary Fault and the Southern Upland Fault is the more likely explanation. The other major structures in the Midland Valley of Scotland, of which the majority are faults, include a set of NE-SW trending faults relating to a reactivation of Caledonoid basement fractures, a set of E-W and ENE-WSW trending growth faults, and a set of NW-SE and WNW-ESE trending faults (Read 1988). The shapes of the N-S trending basins are more synclinal than graben-like and do not occur extensively across the Midland Valley of Scotland to the south and west. Dextral strike slip systems have already been recognised from the late Devonian and Carboniferous of the Appalachians and the European Variscides (Read 1988) and the structures of the Midland Valley of Scotland seem to fit into the same framework. Read (1988) concluded that the structure of the Midland Valley of Scotland was, more likely to be the result of a combination of dextral strike slip movement superimposed on a dominant thermal subsidence, after a period of lithospheric attenuation and crustal rifting along Caledonoid lines. None of the sedimentological findings contradict this model.

The presence of a dextral strike slip regime during the Dinantian is compatible with the evidence, such as the NNE-SSW orientation of the sandstone dykes and the SW direction of overfolds, provided by Cater (1987) from the Granton 'Shrimp-Bed'. The third model of dextral strike slip faulting, which is thought to have occurred in North America at the same time, was accepted as the most likely model by Read (1988).

3.1.3 Palaeo-geomorphology of the Midland Valley of Scotland.

The Lower Limestone Group consists of alternating marine and lagoonal or terrestrial depositional environments. Geikie and Peach (1900) discussed two distinct types of sedimentation which they called the 'lagoon' or 'coal-measure type' and the 'marine' or 'limestone type'. The first type was characterized by sandstones and shales with coal seams, fireclays and ironstones with a fossil content comprising of plant and abundant fish material. The fauna found in these rocks was thought to have lived in enclosed non-marine basins or lagoons of marine water. The second type consists mainly of limestones accumulated in open sea conditions with a distinctive fauna of corals, crinoids, bryozoa, brachiopods and other marine animals. These limestones are usually associated with calcareous shales containing a similar marine fauna. The crustacean-bearing shales of the Shrimp Member lack the non-marine character of the first type, and lack also the normal marine indicators of the second type of sedimentation. This suggests that the fauna is representative of a restricted environment which occurs between the more open marine conditions of the Top Hosie Limestone, and the freshwater conditions at the top of the Manse Burn Formation.

Isopachs of the thickness of sediment in the Limestone Coal Group, proposed by Read (1988), suggest a northern source area for the sandy prograding deltaic sedimentation in the Midland Valley of Scotland, whereas Stedman (1988) argued that due to the lack of evidence for deltaic sedimentation, it was preferable to regard the dominant deposition in the Midland Valley of Scotland as being that represented by a coastal alluvial plain.

Within this coastal alluvial plain, several barriers to sedimentation in the western Midland Valley of Scotland can been recognised. The Pentland Hills Devonian lavas, and the volcanic activity which was concentrated along the Bo'ness Line, may have acted as partial north-south barriers to sedimentation and faunal migrations between the east and west Midland Valley of Scotland (Read 1988). This barrier would have prevented much of the coarser sediments from being transported westwards from the Fife area. Sediment derived from a source to the north of the Kincardine Basin would have entered the western

MVS, increasing the amount of clastic sedimentation in the Kincardine Basin and the Glasgow Basin.

Goodlet (1957) proposed several areas of non-deposition within the Lower Limestone Group of the Midland Valley of Scotland which may have represented islands; an area east of Ayrshire, one in south-west Ayrshire, and another in the Southern Uplands. Richey *et al.* (1930) suggested that prior to the period of deposition of the Hurlet Limestone that there was a barrier between north Ayrshire and the Glasgow Basin, which was later breached to allow a connection to be made between the two areas. Although the barrier was reduced during the Hurlet transgression, and the Top Hosie transgression, local subsidence, north of the Dusk Water Fault and south of the Campsie Fault and Paisley Ruck, prevented the barrier from reforming during the deposition of the Manse Burn Formation. The barrier which developed between the Dusk Water and Inchgotrick faults probably extended westwards, at least as far as Arran, preventing marine water access from the west. The reduction in the thickness of sediments at the horizon of the Manse Burn Formation towards the south on Arran and on the south side of the Dusk Water Fault, supports the presence of this barrier between northern and southern Ayrshire at this time (see Section 3.1.2).

George (1958) suggested that the area of non-deposition in the south-west part of Ayrshire was probably due to post-Dinantian overstep rather than non-deposition. The direction from which marine waters entered the western MVS, during the lower Namurian, is likely to have been from the south west across the southern Ayrshire Basin.

Further evidence for the Dusk Water-Inchgotrick fault block barrier can also be seen in the distribution of the relative abundance of different crustaceans. *Crangopsis*, the brackish water crustacean is more abundant in North Ayrshire, relative to the other crustaceans, with *Palaemysis*, a marine representative, becoming more abundant towards the east (see Chapter 6). *Tealliocaris*, a hypersaline crustacean, *Tyrannophontes* and *Cyclus*, both marine crustaceans, have only been found from localities in the eastern part

between Bridge of Weir and Kilsyth (see Chapter 6). This suggests that the barrier was closed to any marine influence to the west, but more open to the east. The base of the Manse Burn Formation, the Shrimp Member, represents the start of a regression after the initial Top Hosie transgression. This marked the onset of the widespread non-marine deposition of the lower part of the Limestone Coal Group.

3.2 The nature of the Manse Burn Formation sediments across the Midland Valley of Scotland.

The Manse Burn Formation varies greatly in thickness and character across the Midland Valley of Scotland, but its position can be determined from the presence of the Top Hosie Limestone or equivalent across most of that area. The presence or absence of various members of the formation, is mostly indeterminable due to the general paucity of fossils. The Shrimp Member is more easily recognised due to the presence of abundant bivalve spat throughout this member. The Posidonia Member is also easily recognised due by the abundance of the bivalve, *Posidonia corrugata*. The Shrimp Member only occurs in the central area, and the western area north of the Dusk Water Fault, but the Posidonia Member seems to extend further towards the east into Fife and to the west as far as Arran.

Working from east to west, the detailed characteristics of the horizon equivalent to the Manse Burn Formation are as follows: in eastern Fife the Top Hosie Limestone is overlain by a marine shale containing *Bellerophon urei*, *Nucula gibbosa*, *Leperditia okeni*, *Zaphrentis sp.* from an exposure east of St Monans harbour (Geikie and Peach 1902) and a micaceous non-marine shale containing abundant plant material. At Balbougie in southern Fife there is an exposure of a '*Bellerophon* limestone' (=Top Hosie Limestone) which occurs above the tuffs of Charlestown (Peach *et al.* 1910). The Hosies to the west of Charlestown are overlain by black shales (Geikie and Peach 1900) and the Upper Kinniny Limestone (=Top Hosie Limestone) occurs intermittently, but is represented by a marine shale wherever the limestone itself is absent (Forsyth

et al. 1977). The marine shale commonly overlies the limestone as at the St Monans exposure mentioned above. At Elie the Red Limestone (=Top Hosie Limestone) is overlain by a few tens of metres of shale (Cumming 1928). In boreholes, where the Upper Kinniny Limestone (=Top Hosie Limestone) has been recognised, the overlying sediments consist mainly of silts and silty shales (at Callange and Muircambus), although at Dunotter and in the Cowdenbeath area it is overlain by nearly 1.5m of shales (Forsyth and Chisholm 1968).

Table 3.1 Equivalent horizons to the Top Hosie Limestone within the MVS.

	Top Hosie Limestone Equivalent
Southern Fife	'*Bellerophon*' Limestone
	Upper Kinniny Limestone
Eastern Fife	Red Limestone
Lothians	Bilston Burn Limestone
Campsie Hills	'*Bellerophon*' Limestone
East Kilbride	Calderwood Cementstone
North Ayrshire	Hosie 'D'
Muirkirk	McDonald Limestone

The highest exposed limestone in the Skolie Burn, a tributary of the Briech Water in the Lothian regions, which is thought to an equivalent to the Hosie Limestones, is overlain by shales (Peach *et al.* 1910). The basalts in the Bathgate Hills of the Top Hosie Limestone horizon do not extend southwards for any great distance, disappearing before reaching the Almond River 3km to the south. This may be due to the subsurface igneous intrusion having an essentially circular shape (Davidson *et al.* 1984). The lavas probably represented a topographic high during the deposition of the Hosie limestones, and for a short period after (Howell and Geikie 1861, Peach et al. 1910). A bore at Moss-side, near Durhamtoun, revealed a section which included the Top Hosie Limestone overlain by more than 4m of shales, the lower part of which was limey and fossiliferous (Peach *et al.* 1910). In the Midlothian basin the Bilston Burn Limestone (=Top Hosie Limestone) is overlain by a sandstone with occa sional shal y bands (Peach *et al.* 1910; Peach and Horne 1910).

The sediments of the Lower Limestone Group are thicker in the western side of the Kincardine Basin as well as on the downthrown side of the Campsie Fault in the Denny area (Francis *et al.* 1970), although the shales almost disappear in the River Carron near Dunipace north of the Campsie Fault. In the area south of the fault, the Top Hosie Limestone is overlain by a thick succession of shales of between 15m and 24m thickness. To the east the shales overlying the Top Hosie Limestone are thinner (9-15m thick) but are similar in character to the western part of the Kincardine Basin (Francis *et al.* 1970). The increased sedimentation in the western side of the Kincardine Basin may be related to the eastward thinning of the underlying lavas. The eastward increase in the sand content of the sediments, seen in the Glasgow area, seems to continue into the Stirling district. Subsidence rarely allowed the depth of water to become shallow enough for the vegetation to colonize the area at this time (Francis *et al.* 1970).

Clough *et al.* (1911) correlated the '*Bellerophon*' Limestone of the Campsie Hills with the Main Hosie Limestone in the Glasgow area, and suggested that the Top Hosie Limestone was not represented in the northern area. This was later to be disproved due to the presence of abundant *Posidonia corrugata*(of the Posidonia Member), and the '*Bellerophon* Limestone' was later equated to the Top Hosie Limestone (Clough *et al.* 1925; Richey *et al.* 1930; Wilson 1979). The shales above the limestones were thought to have been marine deposits in front of a prograding delta of a large sluggish river bringing suspended organic debris and mud seawards. The shales of the Shrimp Member are best exposed in this area.

At East Kilbride, several localities within the Calderwood Cementstone (=Top Hosie Limestone) which were quarried in the : provided a fauna of shrimps identical to that of Bearsden in content and preservation (Peach 1908, Macnair 1917). This crustacean fauna has been known from East Kilbride since 1885 when Patton and Coutts first recorded its presence. All these localities were found to be infilled leaving no exposure. One possible crustacean fragment was found from a shale tip on the banks of the Calderwood Water (NS66185505). There are, however, some borehole samples housed in the British Geological Survey

in Edinburgh which contain crustaceans from a horizon above the Top Hosie Limestone. Abundant bivalve spat is found associated with the crustaceans in these shales.

Table 3.2 Bore-hole samples from East Kibride (held in the British Geological Survey, Edinburgh).

Locality	Bore	Specimen No.	depth to THL	Fauna
Parkhall St.	3	10E 5826	2.6m	Bivalve spat
				Crangopsis
		10E 5827	2.5m	*Crangopsis*
West Mains	4	ET 6832	2.61m	Bivalve spat
				Crangopsis
		ET 6833	2.61m	*Crangopsis*
		ET 6834	2.46m	*Crangopsis*
West Mains	5	ET 6880	?1.83m	*Crangopsis*
		ET 6881	?1.37m	*Crangopsis*
West Mains	10	ET 7051	?1.22m	*Crangopsis*
		ET 7052	?0.89m	*Crangopsis*
West Mains	11	ET 7094	2.13m	*Crangopsis*
		ET 7095	2.03m	*Crangopsis*
Greenhills	4	2E 1404	3.93m	*Crangopsis**

* Particularly well preserved *Crangopsis*

The Hosie 'D' Limestone (=Top Hosie Limestone) to the south near Dalry is overlain by a marine shale and about 4 metres thickness of the Shrimp Member. The other members of the Manse Burn Formation are much reduced in thickness, or absent. The Shrimp Member is overlain by the Lingula Member at the locality in the Swinlees Glen. The members overlying the Shrimp Member are not exposed at any other locality in northern Ayrshire.

In central Ayrshire the Top Hosie Limestone is overlain by a hard sandy shale in the Wyndy Burn near Nethershield (Eyles *et al.* 1949). In the Muirkirk District the THL is overlain by shales and ironstones (Geikie *et al.* 1873). North of this, at Lesmahagow, the McDonald Limestone (=Top Hosie Limestone) is overlain by thin shales and thick channelled sandstones. In the Glenmuir Water at Nether Guelt the McDonald Limestone is also overlain by thin shales and channeled sandstones. The absence of the Manse Burn

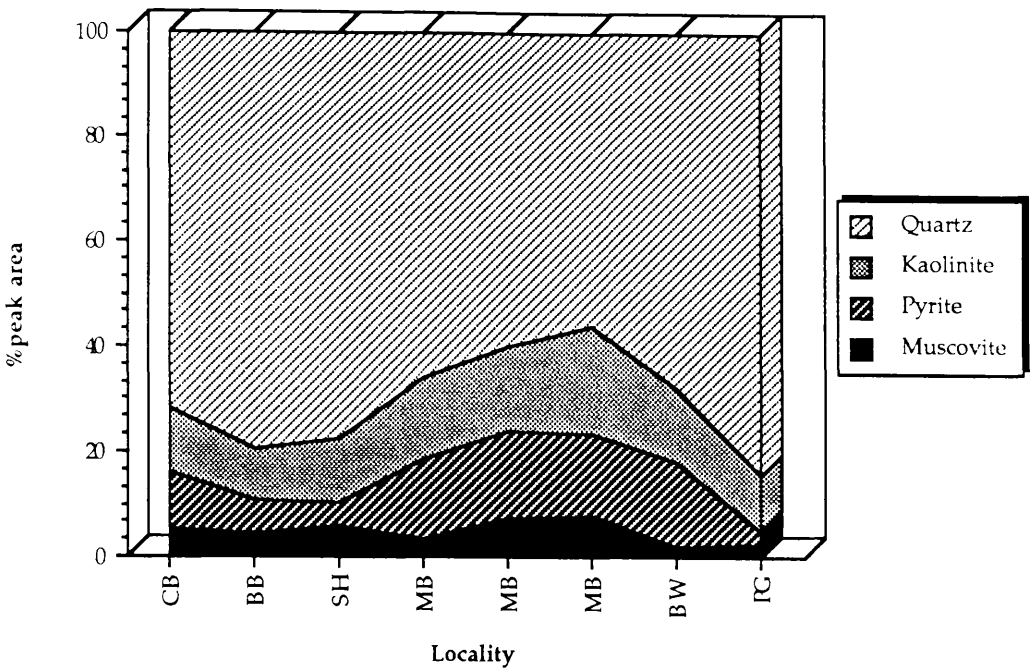
Formation suggests that this area was exposed at this time and represented a barrier to marine influence.

On Arran, the Hosie Limestones are exposed in the Laggan section to the north of the island. The top-most Hosie is overlain by dark micaceous shales, containing abundant plant remains, which are in sharp contact with the overlying sandstone (Gunn *et al.* 1903). The Hosie limestone which is exposed here contains abundant *Posidonia corrugata* and *Lingula*, and may represent the Top Hosie Limestone. The strata between the Hurlet Limestone and the Index Limestone, further south at Corrie, consists mainly of thick sandstones and flags with the occasional shale (Gunn *et al.* 1903)

3.3 Petrography of the Manse Burn Formation with particular reference to the basal members.

The sediments were analysed using X-Ray Diffraction (XRD) techniques to determine the relative abundance of minerals between the members of the Manse Burn Formation (absolute abundances are not used, only the changes in relative peak area). It was found that the sediments of the Shrimp Member had consistent mineral compositions between localities (Fig. 3.4) and that the relative changes between the Shrimp Member and shales of the other members were distinctive (Fig. 3.5). The area beneath the (hkl=101) peak for quartz, the (hkl=001) peak for kaolinite, the (hkl=200) peak for pyrite, the (hkl=001) peak for muscovite, the (hkl=104) peak for calcite, and the (hkl=211) peak for phosphate were converted into percentage peak area and compared between the sediments of the different members. These minerals were the most abundant in the sediments and are easily recognised on the XRD traces (see Appendix A19c, A22-28).

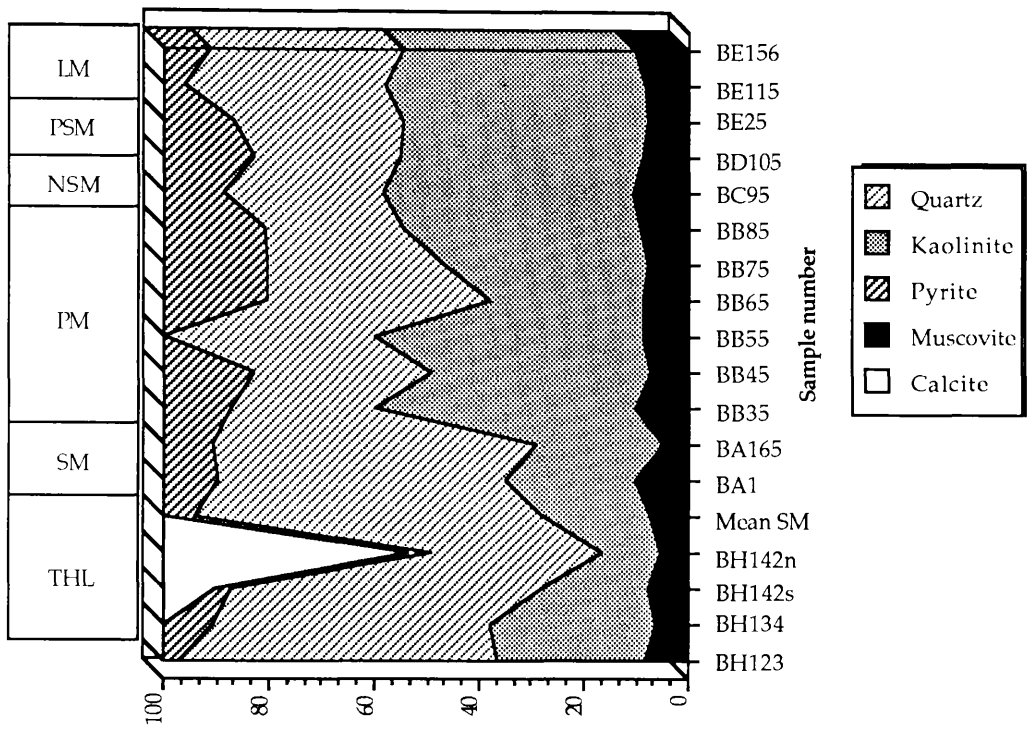
Figure 3.4 The %peak area of the mineral constituents of the Shrimp Member from a variety of localities (CB=Corrie Burn; BB=Burniebrae Burn; SH=Spouthead; MB=Manse Burn; BW=Bridge of Weir; PG=Powgree Burn).



The Posidonia Member contains a greater amount of pyrite and less quartz than the Shrimp Member and contains a greater abundance of benthic organisms. The existence of more marine conditions, in the Posidonia Member, may have resulted in more sulphate reduction within the anoxic sediment to produce a greater concentration of pyrite. The decrease in the quartz indicates a fall in clastic input associated with the onset of more marine conditions. More oxygenated conditions are indicated by the increase in the benthic fauna. Nutrients from freshwater sources would have caused eutrophication in the low energy restricted environment of the Shrimp Member preventing the colonisation of the substrate surface by benthic organisms, but a reduced freshwater influence in the Posidonia Member allows more oxygenated conditions at the sediment/water interface to persist and permit benthic colonisation by *Posidonia corrugata*, other bivalves, and gastropods. In the Nodular Shale Member, the Platey Shale Member, the Betwixt Member, and

the Lingula Member, the concentrations of pyrite and quartz varies more than the kaolinite and muscovite suggesting that the freshwater influences were intermittant.

Figure 3.5 The relative %peak area of the mineral composition of the shales from the Manse Burn, Bearsden, using X-Ray Diffraction (BH=Top Hosie Limestone; SM/BA=Shrimp Member; BB=Posidonia Member; BC=Nodular Shale Member; BD=Platey Shale Member; BE=Lingula Member).



similar to BB55 (Fig. 3.5)

The dark organic muds of the Nodular Shale Member contain no pyrite and no fauna, and are thought to represent periods of rapid deposition, under freshwater conditions, of a distal overbank or crevasse-splay deposit. There is also increased clastic input shown by the increase in the concentration of quartz.

(Plate 4.2d)

Thin sections of the Shrimp Member shales exhibit a mixture of continuous and discontinuous laminae of up to 120 per cm. The fauna does not seem to have been disturbed by currents to cause disarticulation or preferred orientation. This would indicate deposition in a low-energy anoxic bottom water environment. In

the rare nodules, which sometimes occur around enterospirae, the true pre-compaction thickness of the sediment is preserved (Shelton 1962). Bivalves are found with no dislocation of the valves and the cross-sections of burrows do not appear to have been affected by compaction. The true thickness of the laminae is on average 0.625mm suggesting a vertical compaction of 87%. Reducing conditions would have occurred during the periodic decay of abundant organic matter marked by the organic-rich laminae. The dark organic laminae may result from changes in the water chemistry (Müller *et al.* 1972), periodic increases of organic detritus from rivers, or seasonal blooms of algae (Boney 1975).

3.4 Chemistry of the Manse Burn Formation.

Trace elements and rare earth elements held within the shales of the Manse Burn Formation could provide clues to the environment of deposition of the shales, the source of the shales, and the diagenetic history of the pore water chemistries (Krejci-Graf 1964; Dill 1986). The latter is discussed more fully in Chapter 4, and the environment and source of the sediments are discussed below.

The concentration of vanadium was measured by wet chemical techniques (see appendix A). Other trace and rare earth elements were analysed using X-Ray Fluorescence (XRF) techniques.

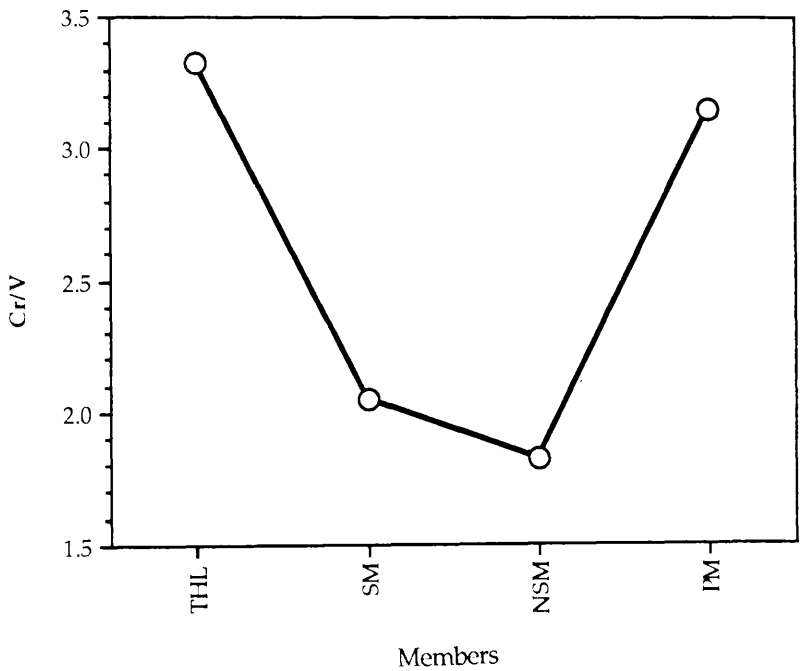
3.4.1 Trace elements, the degree of oxygenation of the sediments and marine water influence.

The relative degree of oxygenation and the environment of deposition of the shales can be determined by the interpretation of several different concentrations, and ratios of concentrations, of different elements (Dill 1986). It may also be possible to deduce the source of the sediments from the trace elements.

The ratios of chromium to vanadium (Cr/V), thorium to uranium (Th/U), as

well as the relative concentration of cobalt, zinc and nickel, provide an indication of the oxygen levels within the sediments. The higher the value of Cr/V the more oxygenated the conditions of deposition of the sediments. As would be expected the highest value of Cr/V occurs in the Top Hosie Limestone, and the lowest value is that found for the black mud from the Nodular Shale Member (Fig. 3.6). The higher concentrations of chromium in the Shrimp Member and the Posidonia Member may be due to being trapped in flocculating colloidal materials common in nearshore environments where mixing of fresh and marine waters occurs (Dill 1986).

Figure 3.6 The Cr/V ratios for sediments from the Manse Burn. The lower the value, the more anoxic the environment of deposition was (THL=Top Hosie Limestone; SM=Shrimp Member; NSM=black mud from the Nodular Shale Member; PM=Posidonia Member).



Similarly, a lower ratio of Th/U is indicative of more anoxic conditions. Normal shales typically have thorium concentrations of about 12ppm with high Th/U values. In black shales, however, there are variable thorium concentrations, but low Th/U values are expected due to lower solubility of

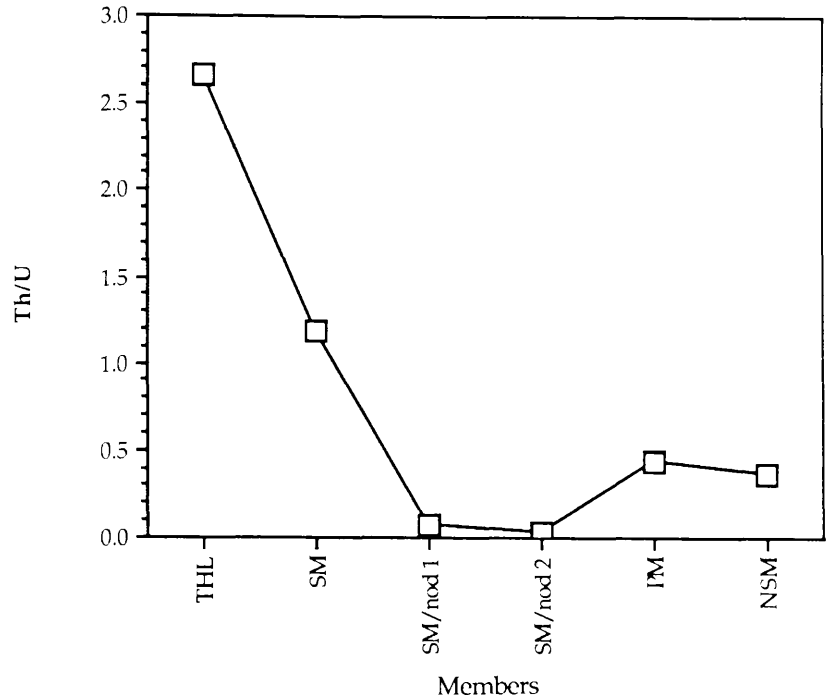
uranium in anoxic waters (Rogers and Adams 1978a, b).

Table 3.3 Concentration of thorium in the sediments of the Manse Burn Formation and a concentrations for sediments quoted from Rogers and Adams (1978a, b).

Sediment	[Th]ppm	[U]ppm	[Th]/[U]
shales	10.2-13.1	2-4.1	2.7-7
black shales	-	3-1244	low
limestones	0.05-2.4	0.35-2.34	0.7-1.1
phosphate rocks	1-5	50-300	<0.1
ocean muds	1-2	0.2-0.7	3-4.5
SM	13	11	1.18
THL	8	3	2.67
PM	8	18	0.44
NSM	4	11	0.36
SM/nod 1	2	27	0.07

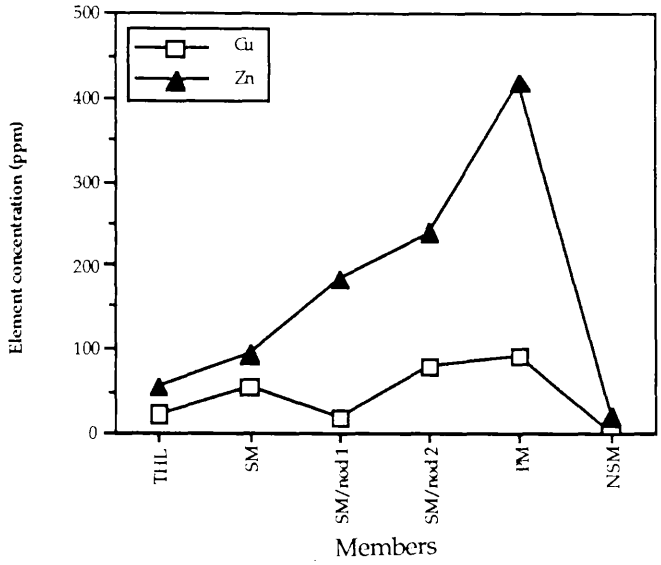
The values for the Shrimp Member (SM) and the Top Hosie Limestone (THL) suggest a more oxidizing environment. The other values suggest reducing conditions and the precipitation of uranium causing low Th/U values for the Posidonia Member (PM) and the black mud of the Nodular Shale Member (NSM). The low Th/U value in the phosphatic nodule from the Shrimp Member (SM/nod 1,2) may be due to enrichment relating to the precipitation of phosphates.

Figure 3.7 The relative Th/U values for the sediments from the Manse Burn, Bearsden. Low values are expected in the more anoxic sediments (Members as for Fig. 3.6).



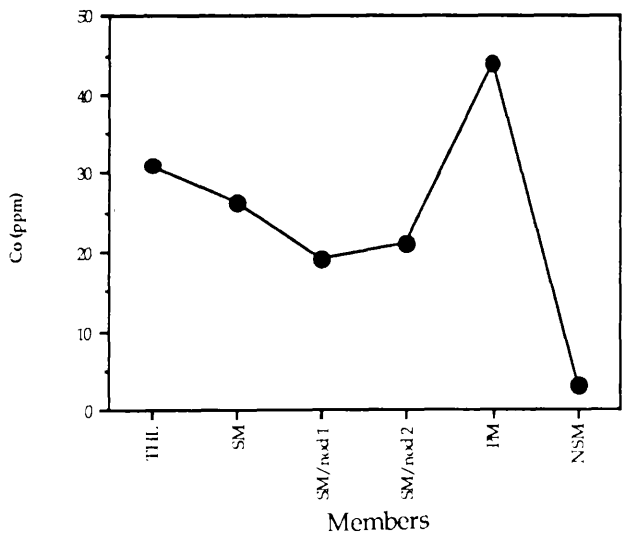
Organic compounds are the main carrier phases of cobalt, zinc, and nickel (Johnston *et al.* 1988) and can also give an indication of the prevalent oxygen conditions of the sediments. Although zinc does not show any particular trend for facies determination, it can be more concentrated, along with copper, in certain animals (Windom *et al.* 1973, Nozaki and Miyahara 1974, Wedepohl 1978a, b). Copper is not affected by the oxygen-deficiency of the water column (Johnston *et al.* 1988). Copper and zinc concentrations can be influenced by secondary pore waters and do not provide reliable results except where they have been fixed by early diagenesis, such as in the Top Hosie Limestone and the nodules from the Shrimp Member. This is due to the copper and zinc occupying exchangeable sites within the expandable clay content of the sediments and are found to be affected by the dialysis in a 1 molar NaCl solution, of a powdered nodule (SM/nod 1=original nodule; SM/nod 2=after dialysis for 48 hours). Nickel, however, does not appear to be affected to any great extent.

Figure 3.8 Concentrations of copper and zinc in the sediments from the Manse Burn, Bearsden(Members as for Fig. 3.6).



The typical values for cobalt concentration in marine shales is 10-160ppm (Turekian 1978a). The cobalt concentration does not vary much for the THL (31ppm), the SM (26ppm) and the PM (44ppm), but is much lower in the black mud of the NSM (3ppm) suggesting anoxic water conditions for this sediment as cobalt tends to be released under reducing conditions.

Figure 3.9 Change in concentration of cobalt between sediments from the Manse Burn, Bearsden. The lower the value the more anoxic the sediment (same Members as Fig. 3.6).



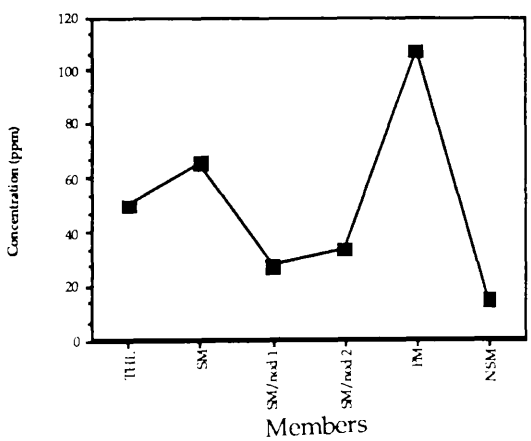
Plants, free living nitrogen fixing bacteria, and blue-green algae require traces of cobalt, copper and zinc for various biochemical reactions (Ray 1972) and may have increased concentration in the sediment, although, cobalt would be released again on decomposition of this organic matter in anoxic environments.

Table 3.4 The relative concentration of Cu, Zn, and Ni after dialysis of a phosphatic nodule.

Sediment	[Cu]ppm	[Zn]ppm	[Ni]ppm
SM/nod 1	18	184	27
SM/ nod 2	78	239	33

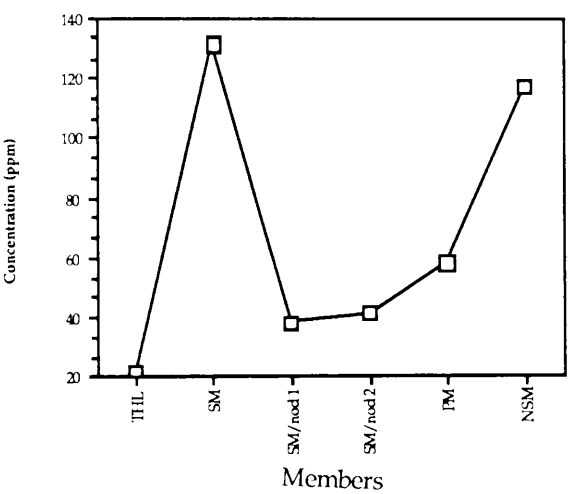
Nickel is lower in fresh water clays (≈25ppm) than in marine clays (≈70ppm) and can be as high as 310ppm in deep sea clays (Turekian 1978b). The nickel concentrations in the sediments from the Manse Burn Formation indicate marine concentrations (THL=49ppm; SM=65ppm; PM=107ppm) except for the black mud from the NSM which has a very low concentration (NSM=14ppm). Cobalt and nickel concentrations are low in the black mud of the NSM due to the absence of pyrite which indicates a non-marine origin for this sediment. The lower values in the phosphatised nodule may be the result of the early phosphate precipitation not allowing the development of pyrite, although, the phosphatisation may have occurred during a period of greater freshwater influence.

Figure 3.10 Relative concentrations of nickel in the sediments from the Manse Burn, Bearsden. The lower values suggest more non-marine conditions of deposition (Members as for Fig. 3.6).



The concentration of rubidium in sea water is higher than that of river waters and, consequently, produces a higher concentration in marine shales than non-marine shales (Heier and Billings 1978). This does not appear to be reflected in the rubidium concentrations in the Bearsden sediments perhaps due to the effect of later pore waters. The original concentration of rubidium in the SM was low (SM/nod 1), but was later readjusted by later pore-waters to produce the present higher values (SM). The possible exchange of ions by pore waters is indicated by the changes in rubidium concentration in the early diagenetic nodule (SM/nod 1, 2) during dialysis, and also by the difference between the concentration in the surrounding shale (SM) and the nodule (SM/nod 1).

Figure 3.11 The concentration of rubidium in the sediments from the Manse Burn, Bearsden (Members are as for Fig. 3.6).



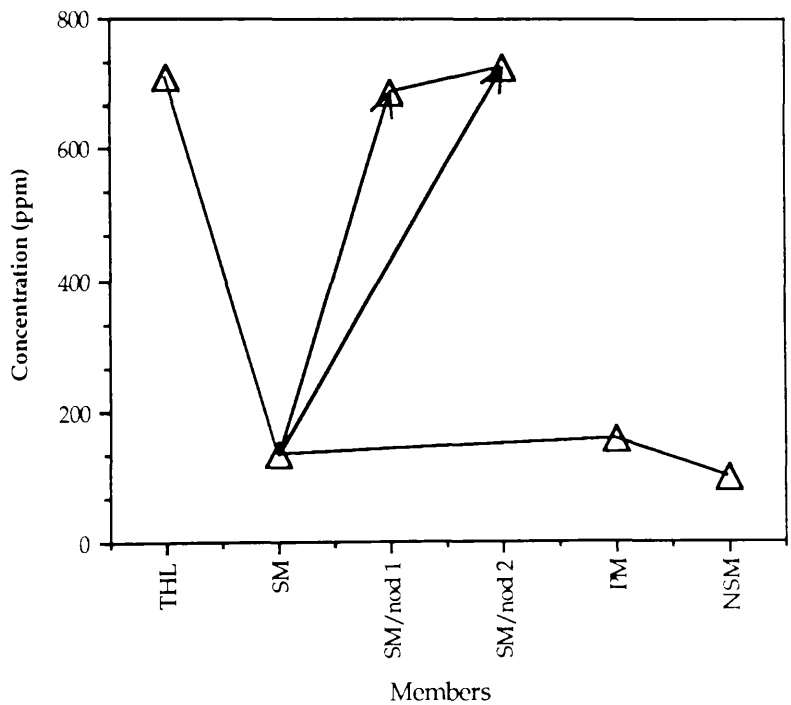
The concentration of strontium in shales may give an indication of the major water source influence (i.e. marine or fresh). Marine waters tend to have a higher concentration of strontium than fresh water which may be reflected in the concentrations within the shales. Typical values for limestones (1460-9769ppm) are higher than marine shales (≈200ppm) (Gieskes 1978). Concentrations of strontium are greater in limestones and phosphorites due to substitution for calcium in the calcite or apatite structure.

The shales (SM and PM) are within the normal range of strontium

concentrations for marine shales. The black mud of the Nodular Shale Formation (NSM) has a lower concentration perhaps reflecting a non-marine low-strontium source.

The limestone (THL) has a low value for a limestone, perhaps due to the high clay content, or a significant non-marine influence. The phosphatic nodule from the Shrimp Formation (SM/nod1, 2) has a strontium concentration within the normal range for phosphorites (200-1025ppm). The phosphate is thought to have precipitated from a phosphate rich pore fluid during an early diagenetic stage following the collapse of the enterospire contained within it (see Chapter 4).

Figure 3.12 The concentration of strontium in the sediments of the Manse Burn, Bearsden. The arrows point to the amount of strontium enrichment due to the precipitation of phosphates in the same sediments (Members are as for Fig. 3.6).



Lead concentrations in sediments may also give an indication of the relative influence of marine waters. Continental waters tend to have higher concentrations of lead than sea water and kaolinite can adsorb high

concentrations of lead (Wedepohl 1978c). Flocculation of clays may cause a higher concentration of lead in shales close to a continental source, than in fully marine shales. The concentration of lead within the sediments from Bearsden is reasonably constant, although, a higher concentration in the black mud of the NSM possibly reflects a more continental influence.

Figure 3.13 Concentration of lead in the sediments from the Manse Burn, Bearsden (Members are as for Fig. 3.6).

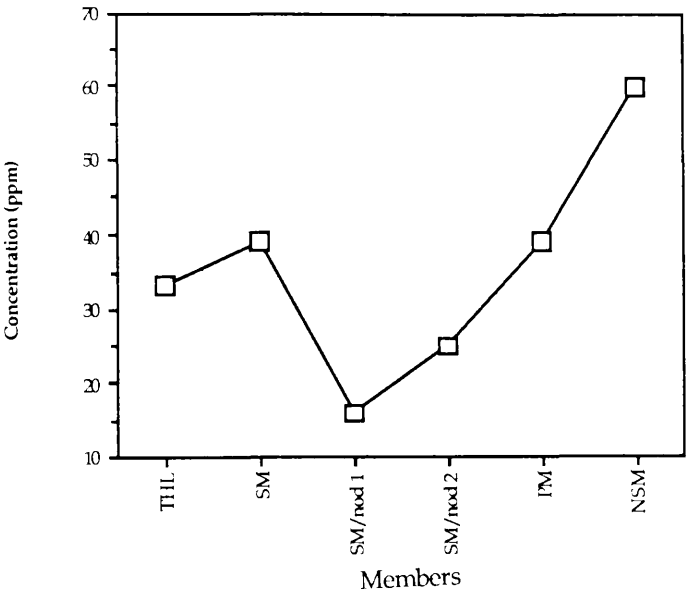


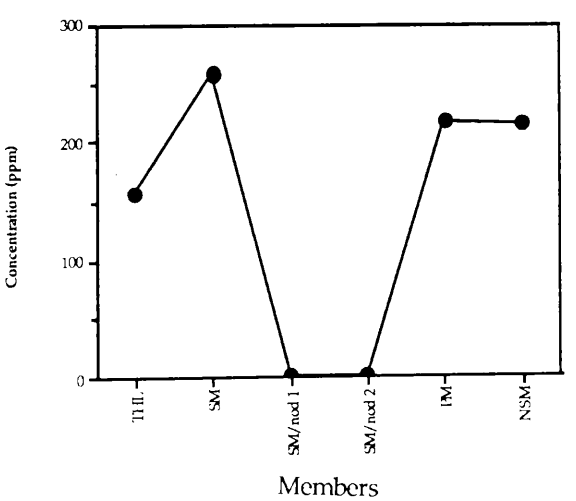
Table 3.5 Concentration of lead in the sediments of the Manse Burn Formation compared to figures quoted for other sediments (Wedepohl 1978c).

Sediment	[Pb]ppm
marine shales	1-139
carbonate oozes	4-219
limestones	0.4-10
evaporites	41-490
SM	39
THL	33
PM	39
NSM	60
SM/nod 1	16
SM/nod 2	25

The higher lead concentration of the shales from the SM and PM may be due to secondary pore fluid cation exchange with the expandable clay content. The original values of the sediment may have been lower as suggested by the sample of the phosphatised nodule (SM/nod 1). The dialysis of SM/nod 1 to produce SM/nod 2, shows that the clays can increase their lead content by cation exchange. The concentration of lead in NSM may also be higher due to cation exchange but, assuming that the sediments are affected by similar pore fluids, the original lead concentration would still have been higher.

Barium is often found in the form of fine particulate barite which can precipitate by biological activity and also from hydrothermal activity near mid-ocean ridges (Bishop 1988). No known phytoplanktonic source is yet known for the biological precipitation of barite from solution although the benthic protozoan *Xenophyophora* is known to precipitate barite (Bishop 1988).Barium can concentrate in decaying organic matter such as faecal debris where there is an increase in the sulphate concentration (Dehairs *et al.* 1980). Barite tends to be concentrated below equatorial zones of high productivity and also in microenvironments rich in decaying organic matter (Bishop 1988). The concentrations are much lower in nearshore clays (18-62ppm) than in deep sea clays (≈750-4000ppm) and can also be quite low in carbonate rocks (Puchelt 1978)

Figure 3.14 The relative concentration of barium in the sediments from the Manse Burn, Bearsden (Members as for Fig. 3.6).



The barium may have entered the sediments by secondary pore waters derived from the subsurface hydrothermal weathering of the barium-rich Carboniferous lavas of the Campsie Hills (section 3.3.3). The barium is non-existent in the early diagenetic phosphatised nodule but is highly concentrated in the enterospirae which contain secondary pore water cements in the large pore spaces left by soft-tissue decay and cracks caused by forced fluid injection (see Chapter 4).

Table 3.6 Results of the trace element analysis with respect to environmental conditions within the Manse Burn Formation and the Top Hosie Limestone (ox=aerobic; an=anaerobic; m=marine; n.m.=non-marine; v.=very; l=low or partially).

	Cr/V	Th/U	Co	Ni	Rb	Sr	Pb
THL	ox	ox	ox	l.m.	m	m	m
SM	an	l.ox	l.ox	l.m.	n.m.	m	m
SM/nod	-	an	l.ox	n.m.	m	?m	m
PM	ox	v.l.ox	ox	m	m	m	m
NSM	an	an	v.an	n.m.	n.m.	n.m.	n.m.

The THL and the PM were deposited in dominantly aerobic marine waters, the NSM was deposited in a freshwater anoxic setting, and the SM was deposited in an environment which was neither fully marine nor freshwater, and not fully anoxic.

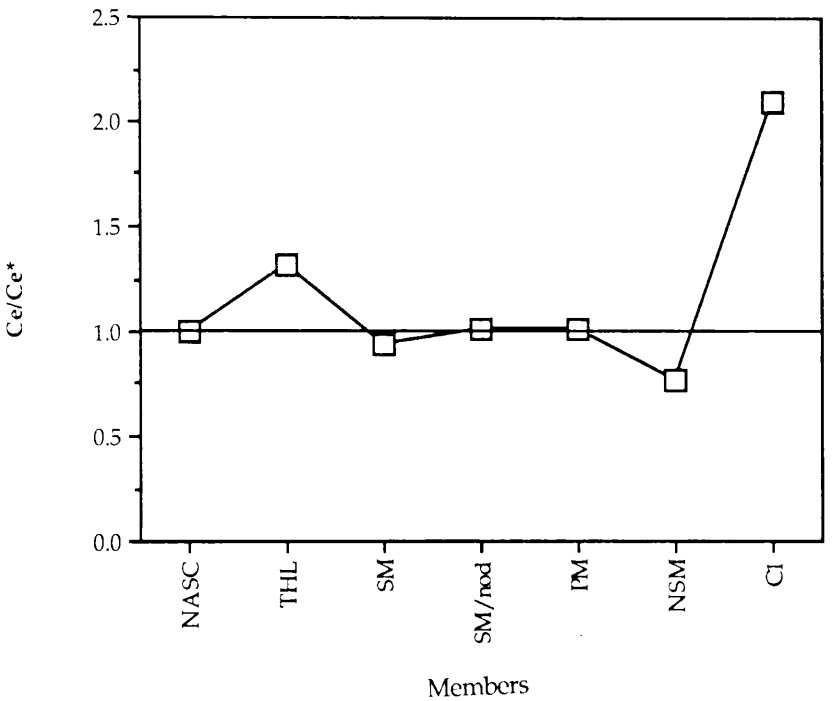
3.4.2 Rare Earth Elements.

The rare earth elements (REE) are representative of the crustal rocks being eroded into the depositional areas. Yttrium has a similar chemistry to the lanthanides and is therefore included in the lanthanide group (Felsche and Hermann 1978). The shales from the Manse Burn Formation are thought to be derived from the erosion of the large Laurasian continental area to the north. The REE, cerium and lanthanum, from the shales of the Manse Burn Formation (MBF) and the Top Hosie Limestone are compared to the North American Shale Composite (NASC) to test this hypothesis. If the values of Ce/Ce* ($Ce+La_{(NASC)}/La+Ce_{(NASC)}$) from the MBF are close to that for NASC, then

it is likely that the shales were derived from the erosion of a large continental area.

The averaged Ce/Ce* anomaly for the Shrimp Member (SM, SM/nod), the Posidonia Member (PM) and a black mud from the Nodular Shale Member (NSM) is very close to unity.

Figure 3.15 The relative enrichment of cerium relative to NASC for some sediments, a nodule (SM/nod), and an enterospire (C1) from the Manse Burn, Bearsden (Members as for Fig. 3.6).



Apatites tend to concentrate the lanthanides (Y≈300X; Ce>1000X; La>1000X) (Felsche and Hermann 1978), as can be seen from the higher concentrations in the phosphatised nodule (SM/nod 1, 2). This, however, should not affect the original Ce/Ce* ratio of the sediments, unless the phosphatisation had resulted from a late pore-water cementation. As the phosphatisation is is an early event, the phosphatised nodule should record the original Ce/Ce* ratio.

Table 3.7 The concentration of lanthanides in the Manse Burn Formation.

Rock type	[Y]ppm	[La]ppm	[Ce]ppm
limestone	4-23	3-10	2-20
shales	16-66	28-79	49-152
SM	31	46	93
THL	44	33	93
PM	47	39	85
NSM	15	39	64
SM/nod 1	777	504	1090
SM/nod 2	870	552	1208
C1	2726	523	2356

The concentrations of the lanthanides are high in the phosphatic samples (SM/nod 1, 2 and C1) as would be expected. However the value of Ce/Ce* for the early diagenetic phosphatic nodule (SM/nod 1, 2) is equal to NASC, despite the high concentrations.

The accumulation of high lanthanide concentrations in fish material is unlikely to have been *in vivo* (Felsche and Hermann 1978), although, the Ce/Ce* value may be representative of the water in which the fish lived. The enrichment in cerium of the enterospire (C1) suggests that the fish lived in waters which were also enriched in cerium, such as would be found in the marine surface waters (De Baar *et al.* 1983), although, seawater is generally depleted in cerium (Gromet *et al.* 1984, Elderfield and Greaves 1982).

The rare earth elements indicate that the sediments were derived from the erosion a large continental source area as the Ce/Ce* ratio values are close to unity.

3.4.3 Source of the sediments.

The results of the trace element analyses suggests that the conditions present in the Midland Valley of Scotland at the time of the deposition of the shales above the Top Hosie Limestone could be that of an initial rift valley (Dill 1986). The structural data, however, does not support this, although there is

some evidence for crustal rifting in the Devonian (Read 1988). Erosion of the Devonian volcanic rocks related to a possible initial rifting in conjunction with erosion of Carboniferous volcanic rocks will have an influence on the trace element composition of the shales. The trace element abundances in the phosphatic nodule from the Shrimp Member shows a similar pattern to that of the nearby Lower Carboniferous vents (MacDonald and Whyte 1981) except for the barium concentration, and the elements normally concentrated in phosphates minerals. The barium concentration represents a secondary pore water concentration derived from the lavas after the phosphatisation event. A small proportion of the elements (Cu, Zn, Pb, Sr) are contained within expandable clays where they can readily exchange with surrounding waters, and therefore, cannot be used reliably in any determination of source (see Figs. 3.16, 3.17).

The trace element profile of the compacted shale from the Shrimp Member (SM) may be related to pore waters from the weathering of the underlying lavas transported by fractures, faults and intergranular pores. The trace elements are still characteristic of an early rift regime although it is best to consider the volcanics as 'within plate' continental or ocean island basalts (MacDonald and Whyte 1981) as the tectonic regime is that of dextral strike slip and not rifting (Read 1988).

Figure 3.16 The relationship between the trace elements of the early diagenetic nodule from the Shrimp Member, and the mean concentrations in the Carboniferous volcanics (calculated from MacDonald and Whyte (1981)). Zinc and zirconium show the greatest difference in concentration between the early diagenetic nodule and the mean volcanics. Copper, lead, and zinc are affected more by pore waters and show a significant shift between the values for the early diagenetic nodule prior to (SM/nod 1), and after dialysis (SM/nod 2).

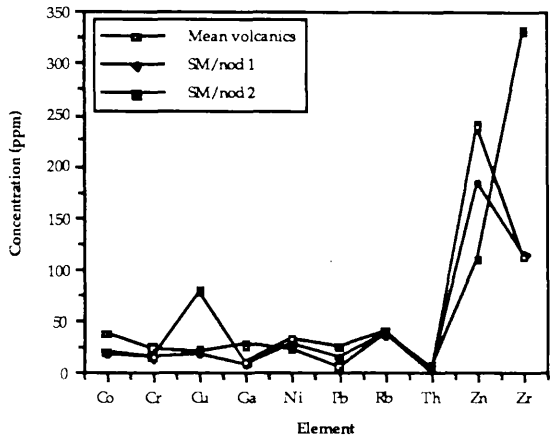
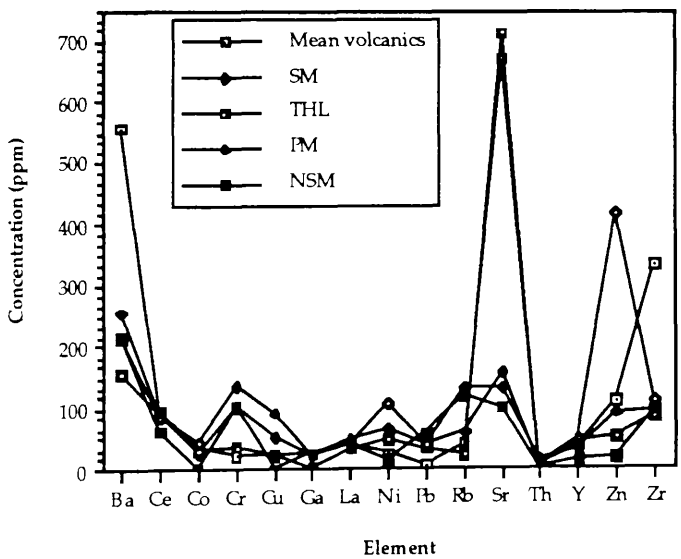


Figure 3.17 The trace element profile of the sediments from the Manse Burn, Bearsden and the mean Carboniferous volcanics (calculated from MacDonald and Whyte (1981)).



3.5 Sedimentary environment of the Manse Burn Formation with particular reference to the Shrimp Member.

The relationship between the fossil assemblages of the different members of the MBF and the sediments is discussed here in order to provide a guide to changes in the general environmental conditions. The detailed spatial and vertical distribution, as well as the orientation, of the fossil organisms recorded during the excavation of the Bearsden site (Wood 1982), is discussed in Chapter 6, and the systematic palaeontology of the crustaceans is discussed in Chapter 5.

The relative concentrations of crustaceans from the Shrimp Member, which was estimated for each locality, shows a greater diversity of genera in the Campsie Hills localities and a lower diversity in the northern Ayrshire localities. The higher diversity of the crustaceans close to a source for freshwater influence suggests that the crustaceans were either, capable of tolerating a wide range of salinities, or, were able to migrate seaward during periods of lower salinity (Valentine 1983). The reason for the higher diversity may be due to increased productivity at the zone of maximum mixing between fresh and marine waters (see Chapters 4 and 6). The more benthic crustacean genera, such as *Tealliocaris*, and *Minicaris*, and the nectonic crustacean *Crangopsis*, may have been more tolerant of a wider range of salinities than the benthic crustacean *Tyrannophontes*, and the nectonic shrimp *Palaemysis* (see Chapter 6).

Bivalve spat are ubiquitous throughout the Shrimp Member as well as within some of the other members. The environmental conditions prevented the bivalves from reaching maturity, although the two, or three, growth stages represented suggests that they were able to grow to some extent before anoxic benthic conditions killed them. The two growth stages in the Shrimp Member, represent two spat falls, an early spat fall which was allowed to survive until the second spat fall which occurred just prior to the period of anoxic benthic conditions. Assuming that the bivalve spat produced a bi-annual bloom, then the eutrophic conditions producing the anoxic benthic conditions was an annual

event. Seasonal rainfall in the catchment area of the rivers feeding greater quantities of nutrient-rich freshwater into the MVS would produce this annual eutrophication. In the Posidonia Member three growth stages are represented, perhaps due to less freshwater influence brought on by avulsion, i.e. a switching of the direction of freshwater flow into the area, and by the development of more oxygenated conditions.

Although there are no marked seasons in the equatorial regions, the northern rivers were probably very large and may have been affected by seasonal rainfall in their catchment area. This would affect, seasonally, the clastic, organic, nutrient, and freshwater input into the Carboniferous MVS. The amount of clastic input into the MVS appears to be dominated by the rate of subsidence and compaction of the sediments (Read 1988). The increase in organic input is not coupled with an increase in the clay input suggesting that the sources for these two components are mutually exclusive. Due to the distance from the open sea and as a result of the interpretation of the chemical composition of the shales, it seems likely that most of the shales were derived fluvially from the weathering of the nearby volcanics. The organic content of the shales may be determined by the seasonally increased nutrient input from a fresh water source into the dominantly marine waters of the MVS at this time (see Chapter 4).

It is impossible to find a modern, or indeed a stratigraphically younger, equivalent of the environment represented by the Manse Burn Formation, as the environmental conditions present were unique to that period and depended on the distribution and position of the continents, the catchment area of the rivers, and the tectonic environment. While the precise environmental equivalent of the Manse Burn Formation may not be present in the modern environment, it is possible to infer from modern environments what some of the characteristics may represent in sedimentological terms.

Concentration of crustacean moults occurs in the back-barrier lagoon of the Mgeni estuary of southeast Africa (Cooper 1988) in an environment bypassed by strong tidal currents where suspension settling leads to the accumulation of

organic rich mud and sand shows some similarity to the Shrimp Member of the Manse Burn Formation. The major differences between this environment and that of the Shrimp Member is that the organic lamination is destroyed by bioturbation, the area represented by this environment in the Mgeni estuary is much smaller, and it occurs in a subtropical region.

The mud facies of the back-barrier association in the Lower Cretaceous Jydegård Formation (Noe-Nygaard and Surlyk 1988) also shows similarities with the Manse Burn Formation. The dinoflagellate blooms caused seasonal mass mortalities of opportunistic faunas, and anoxic conditions caused the formation of finely laminated sediments. These sediments, however, were very shallow and developed rootlet beds in places. The scale of this deposit is comparable to that of the Manse Burn Formation as some of the muddy horizons can be traced laterally for over 1km.

The palaeoecology of the shales immediately below the Top Hosie Limestone has been described as being from a shallow subtidal deposit where current strength was the major factor in determining the faunal assemblages found (Craig 1954). The presence of *Posidonia* was thought by Craig to indicate tranquil and anaerobic conditions in these shales. In the Posidonia Member, however, there are a number of benthic organisms, such as gastropods, which co-occur with the mobile *Posidonia*, indicating that conditions were more aerobic than in the shales below the Top Hosie Limestone. Further up succession in the Manse Burn Formation, the Lingula Member contains a fauna similar to that of the *Lingula-Nuculopsis* community of Craig (1954). According to Craig, this community lived in an environment with higher current strength and more aerobic conditions. As the character of the sediments does not change much, except the degree of lamination development and organic content, within the Manse Burn Formation, it is thought that the faunas are more influenced by the salinity conditions and oxygen levels of the water and sediments, rather than by the strength of the currents.

The general nature of the sediments of the Manse Burn Formation is similar to that of a Yoredale Cyclothem (Dunham 1950, Johnson 1962). The limestone base

of the section could be taken to be the Top Hosie Limestone. The marine shales are represented by the named members of the Manse Burn Formation which are overlain by unfossiliferous ferruginous shales. The top of the Manse Burn Formation is a transition from the fine unfossiliferous shales into sandy shales and finally into a thick sandstone unit. Above the sandstone there is are some silty shales which eventually develop into a seat earth and a coal (Kilsyth Coking or Main Coal in the north).

Table 3.8 Typical Yoredale Cyclothem (Dunham 1950, Johnson 1962).

7) coal
6) ganister or underclay
5) sandstone
4) sandy shale, shaley sandstone or grey beds (interbedded siltstones and sandstones)
3) unfossiliferous (?)non-marine ferruginous shale
2) marine shale
1) limestone

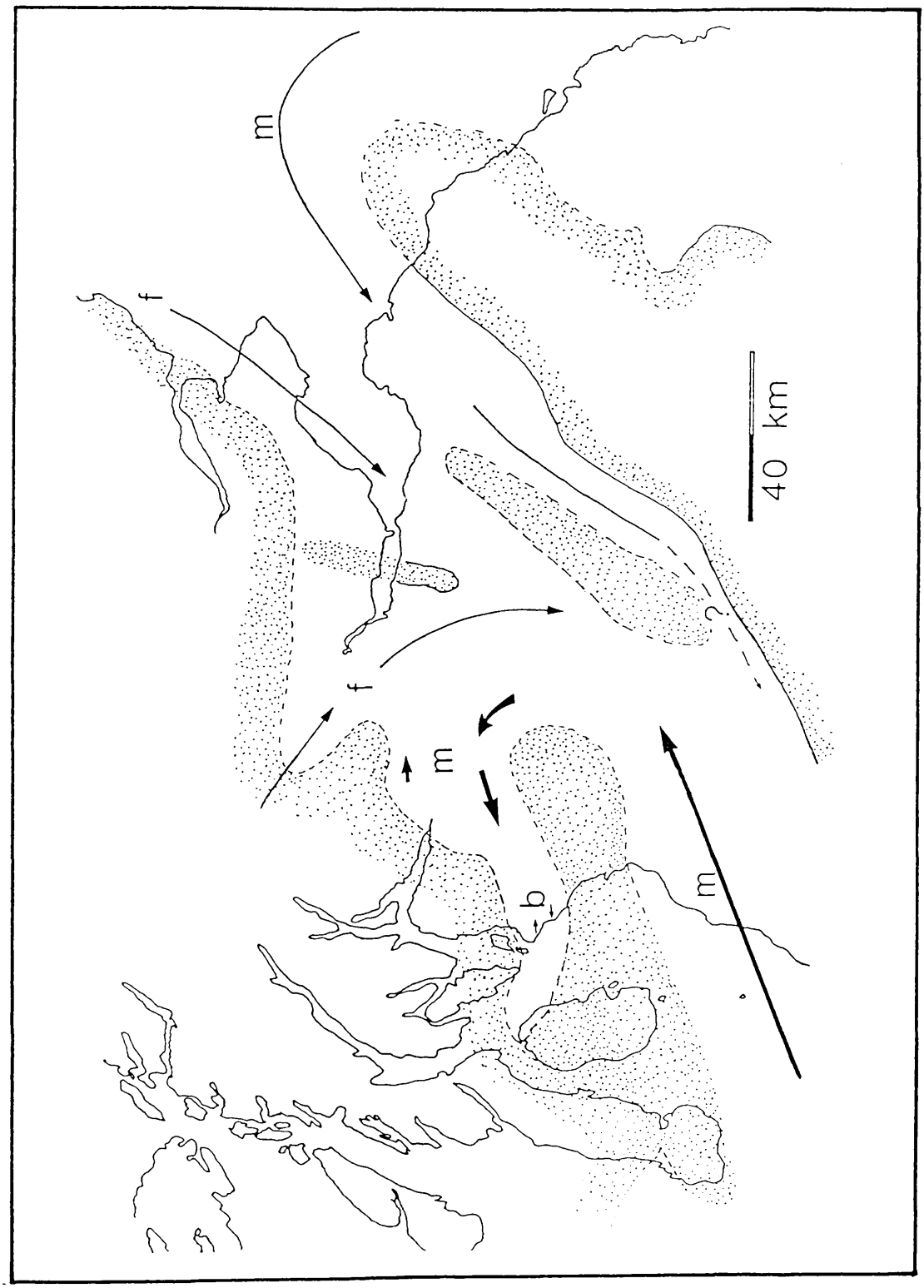
The coal may not be of the same cycle, as the rate of subsidence does not allow the development of distinct and small scale rhythms which can be seen in the condensed sections of the Muirkirk area in the south (Lumsden 1967), and the Dunipace area to the north. The Manse Burn Formation may be represented by a number of weakly developed minor rhythms which do not form complete cycles. The character of the cyclothem represented here is similar to that described by Johnson (1962) for the Carboniferous of Northern England, as being developed on the boundary between Zone 2 (Yordale facies) and Zone 3 (open sea facies). The thickness of the shales in the Manse Burn Formation (≈40m at Corrie) suggests that subsidence was an active force in the development of the shales in the area covered by this formation.

The succession within the Manse Burn Formation is that of a gradual marine regression after the rapid marine transgression represented by the Top Hosie Limestone. This regression is punctuated by several minor marine transgressions, such as that represented by the Posidonia Member and several smaller

incursions represented by shelly horizons within the other members. The rapidity of the incursions be may due either to tectonic activity, especially in the more widespread horizons such as the Top Hosie Limestone, or avulsive events represented by the more restricted horizons, such as the Posidonia Member.

The geomorphology of the Midland Valley of Scotland during the early Namurian suggests that the shales of the Manse Burn Formation were deposited in a partially enclosed body of water with only restricted access to the open sea to the west, and fluvio-deltaic influence to the east. It may be appropriate to regard the sediments as having been deposited in a large back-barrier lagoon beyond the range of tidal influence, but where there were significant seasonal marine and freshwater controls on the salinity and oxygen levels.

Figure 3.18 Palaeogeographical map of the Midland Valley of Scotland during the deposition of the Shrimp Member showing possible surface currents, m=marine; b=brackish; f=fresh.



Chapter 4

Diagenesis and Preservation of Fossils

Many of the fossils from the Shrimp Member of the Manse Burn Formation have been diagenetically altered and most preserve little of their original composition or structure. The best form of preservation results from the early diagenetic phosphate replacement of the cuticle and soft tissues in the eumalacostracan crustaceans. The phosphate has replaced the cuticle in such a way as to preserve the microcuticular structures such as the major subdivisions of the cuticle, cuticular ducts, and pore canals. Early diagenetic phosphatisation of fossil organisms is uncommon, but not unknown (Briggs and Clarkson 1983, Briggs *et al.* 1983, Müller and Walossek 1985, Briggs and Clarkson 1985a, b, Allison 1988b, Martill 1988), although details of the processes of diagenetic phosphatisation themselves, and chemical analyses of the resultant phosphates have yet to be fully explored.

Enterospirae show a range of diagenetic fluid compositions relating to the initial decomposition of the gut and gut contents, phosphatisation, and to later pore water diagenesis. The phosphatisation of the enterospirae is not related to the phosphate content of the water column, but derives primarily from the decomposition of the gut, and gut contents, by bacterial action. Early collapse of some enterospirae, soon after burial, causes an enveloping phosphate nodule to form by the diffusion of phosphates into the sediment.

The bacteria or chemical processes responsible for the phosphatisation of both the crustaceans and the enterospirae produce microspherical aggregates of phosphate approximately 2μm in diameter. The phosphatisation may have occurred within weeks of being deposited on the substrate surface. Increases in nutrient levels associated with the freshwater influxes within the back-barrier lagoon (see section 3.6), would result in algal blooms and eutrophication. On decomposition, the algae would liberate a large enough quantities of available phosphates to allow the phosphatisation of crustaceans for a limited period. Crustaceans on the substrate surface at other times would not

become phosphatised, but would decay to form calcite microconcretions.

Some of the eumalacostracan crustaceans are preserved as thin films of drusy calcite with little or no cuticular structure preserved resulting from decalcification followed by a later pore-filling calcite. The bivalve spat are also decalcified, with only external impressions of the valves remaining. Many other bivalves have secondary recrystallised drusy calcite and some are replaced by pyrite. Myodocopid ostracodes are preserved in outline with the shell replaced by platelets of calcite which form in a similar manner to the calcite microconcretions, which are found in extant eumalacostracan crustaceans as a result of the chitinolytic bacterial decay and recrystallization of the cuticle.

4.1 Phosphate preservation of crustaceans.

4.1.1 Chemistry of phosphates.

The phosphates which form the main constituent of the enterospirae, the crustacean cuticle, and the phosphatic nodules have similar unit cell dimensions. These unit cell dimensions are also similar to previously described analyses for fluor-apatite and carbonate-apatite (Deer *et al.*1978). The cuticle of *Palaemysis* has been analysed using X-Ray Diffraction (Table 4.1, Fig. 4.1). Previous studies using this technique have suggested that the cuticle is composed of fluorapatite. The phosphates which form the main constituent of the Carboniferous crustacean cuticle do have similar unit cell dimensions to fluor-apatite and also to carbonate-apatite (Deer *et al.* 1978). The apatite described by Rolfe (1962) in the cuticle of *Ceratiocaris papilio*, also has similar unit cell dimensions (Table 4.1).

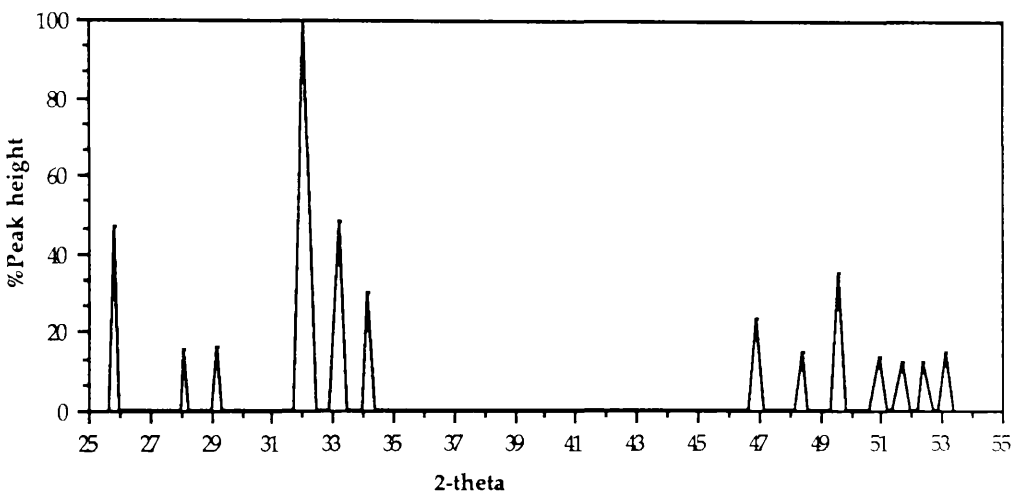
The unit-cell *a* values for the cuticle of *Palaemysis* are closer to younger unaltered francolite values for unit-cell *a* (Miocene of Mexico 9.335-9.340) than to older values (Permian of western United States 9.350-9.355, Ordovician of Tennessee 9.340-9.350) (McClellan 1980). There appears to be a general increase in the unit-cell *a* dimension through time due to the restructuring of the

phosphate structure (McClellan 1980). This suggests that the structure of the phosphate of the cuticle of *Palaemysis* may not have altered much.

Table 4.1 The unit cell dimensions of phosphates from the Manse Burn Formation.

a	c	c/a	Source
9.337±0.0086	6.885±0.0053	0.737	*Palaemysis* (Hewitt *pers. comm.*)
9.344±0.0056	6.891±0.0056	0.737	*Palaemysis* (Whyte *pers. comm.*)
9.339±0.0013	6.883±0.0028	0.737	*Palaemysis* cuticle
9.334±0.0018	6.876±0.0013	0.737	enterospire C1
≈9.35	≈6.88	≈0.736	*Ceratiocaris papilio* (Rolfe 1962)
9.35	6.87	0.735	Fluor-apatite (Deer *et al.* 1978)
9.34	6.88	0.736	Carbonate-apatite (Deer *et al.* 1978)

Figure 4.1 Typical XRD trace of phosphates from the cuticle of *Palaemysis*.



Energy Dispersive System (EDS) probe analyses of the cuticle suggest, however, that the composition is more complex. The basic phosphates formula for the fossil crustacean cuticle is

$$(M)_5(X)_3(Z)$$

(M=Ca, Na, Mg, Fe; X=PO_4, CO_3, SO_4, OH; and Z=F, Cl, OH). The composition varies greatly but usually contains significant amounts of calcium, phosphorus, chlorine, and sodium. The classification of the phosphate, either francolite or dahllite, depends on the relative amounts of CO_3^{2-} and F^- (Deer *et al.* 1978).

The analysis of CO_3^{2-}, OH^-, and F^- was beyond the analytical scope of the EDS probe used. However the average sodium content of the phosphate is high, as it is in francolite, and thus the cuticle phosphate is held to be that mineral.

Strontium or the rare earths, predominantly cerium, may replace calcium to a considerable extent. Values of up to 11% strontium are known in some fluor-apatites (Deer *et al.* 1978). The phosphates of the enterospirae showed that these elements were enriched relative to NASC (La* and Ce*). In the phosphate nodule, however, the rare earth elements are not enriched relative to NASC. This indicates that the enrichment may have occurred within the enterospirae by differential adsorption of the elements within the living animal or bacterial decomposition of the gut soon after death rather than by later diagenetic effects (Table 4.2).

Table 4.2 Concentration of rare earth elements and strontium in phosphates from the Shrimp Member.

Sr (ppm)	Ce (ppm)	La (ppm)	Ce.La*/La.Ce*	Source
1161	2356	523	2.10	enterospire C1
416	275	23	5.58	enterospire C2
688	1090	504	1.01	nodule A/N
132	93	46	0.94	shales (Shrimp Member)
142	66.7 (Ce*)	31.1 (La*)	-	NASC

Secondary phosphate, commonly francolite, has a higher Ca:P value than many organically fixed phosphates (Aldridge and Armstrong 1981). The Ca:P values for Carboniferous crustaceans (Table 4.3), however, have a range between that for primary phosphates, and for francolite. The use of Ca:P ratios in the differentiating secondary from primary phosphate is unreliable and, in this case, may be a function of the thickness of the cuticle exposed to the available phosphates (Fig. 4.1).

Table 4.3 Ca:P values for a variety of fossil phosphates.

Organism	Source	Ca:P
Spherical microfossils	Aldridge and Armstrong (1981)	1.99-2.12
Conodont	"	2.19
Francolite	"	2.5-2.7
Tealliocaris	This study	2.33-2.44

Figure 4.2 The relationship between the cuticle thickness and the Ca:P ratio.

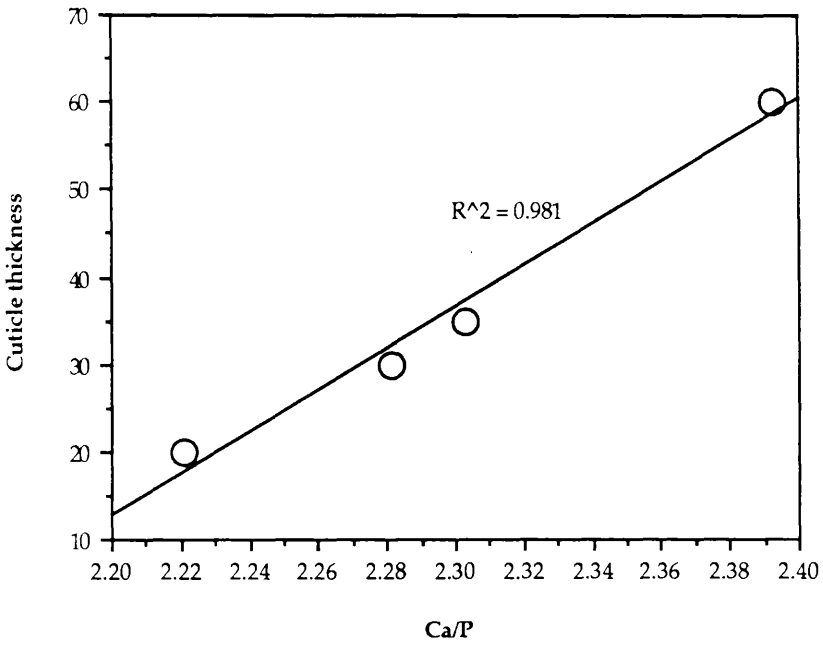
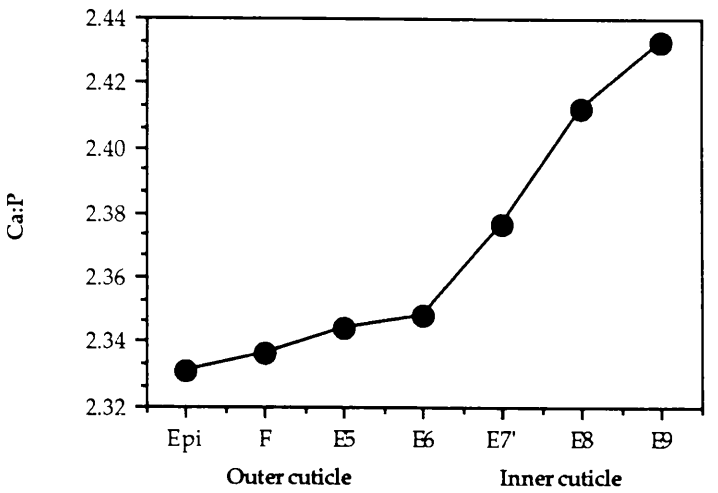


Figure 4.3 Traverse across the cuticle of *Tealliocaris* showing the variation in Ca:P.



As would be expected, the lower Ca:P ratios occur in the outer cuticle where the cuticle is in direct contact with the phosphate-rich waters (Fig. 4.3). Crustaceans with thicker cuticle retain more CO_3^{2-} in the inner cuticle as less phosphate ions are able to penetrate the full thickness.

4.1.2 Controls on the composition of francolite.

The composition of francolite may be controlled by a number of factors (McArthur 1985) such as:-

1) the pH and composition of the solution from which the francolite forms;
2) weathering by meteoric waters;
3) diagenetic and catagenetic alteration as a result of burial, presumably as a result of increasing pressure and temperature;
4) metamorphism producing more fluorapatitic compositions;
5) the original composition of the material being replaced.

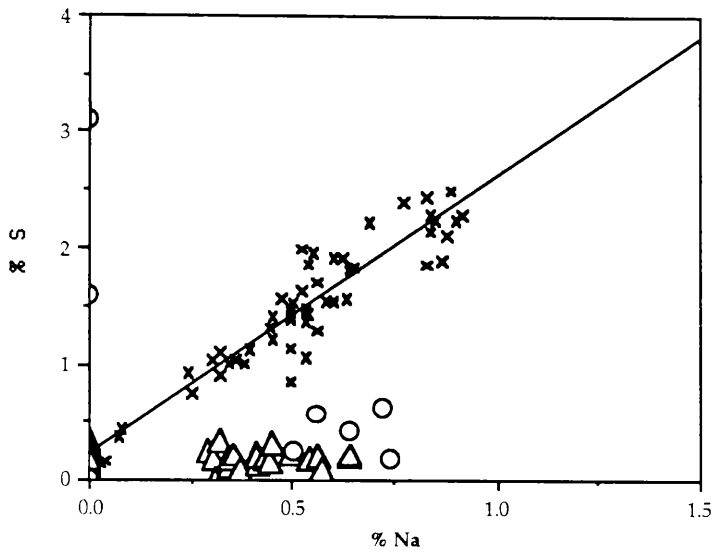
The substituent elements of francolite are neither thought to be structurally nor mechanically controlled, nor significantly affected by the rate of francolite

formation (McArthur 1985). The mechanism by which the francolite forms may not affect the composition, but it may affect the morphology of the phosphates produced. Francolite may form by precipitation from anoxic pore-waters (Bremner 1980, Benmore *et al.* 1983), by replacement of carbonate (Parker 1975), by bacterial processes (Lucas and Prévot 1984), and by precipitation from the water column at the sediment-water interface (Sheldon 1981). The phosphatisation of crustaceans from the Shrimp Member is likely to have resulted from carbonate replacement at the sediment-water interface, perhaps with the help of the post-mortem precipitation of francolite in phosphorus-rich bacterial cells (O'Brien *et al.* 1981).

The composition of the francolite in the cuticle of the fossil crustaceans was not affected by metamorphism or burial, as the conodont colour alteration indices for the Carboniferous in the MVS suggests a maximum overburden of 3000m, although it is more likely to have been closer to only 1000m (Dean 1987). The only factors which may have affected the composition of the francolite, in the case of the fossil crustaceans, are the original composition of the shell, the composition of the waters in which the francolite precipitated, and later pore-water weathering effects.

The effect of weathering is to produce a more fluorapatitic composition by the removal of the substituent elements, such as Sr, Na,and SO_4, although the X-ray $CO_2.F/P_2O_5$ and the Na/SO_4 ratios are not significantly affected (McArthur 1985). The small amount of sulphur and sodium in the cuticle of the fossil crustaceans, as well as in the enterospirae (Fig. 4.4), suggests that there has been some removal of these elements from the original francolite structure due to weathering. The ratio of sodium to sulphur, however, is much higher than that recorded for phosphorites (McArthur 1985), which would suggest a higher original sodium concentration in the formation waters. This, of course, assumes that the concentrations were derived from formation waters rather than being the original concentrations in the cuticle.

Figure 4.4 Variation of Na with SO_4 in francolite. Crosses represent data presented by McArthur (1985, Table 2); open circles represent probe data of enterospirae groundmass; open triangles represent probe data of fossil crustaceans from the Shrimp Member.



The detailed structures preserved in the crustacean cuticle (section 4.1.3, and Plate 5.13), suggests that little diagenetic recrystallization, which would occur during weathering, has taken place. This suggests that the substituent composition of the francolite should be a reflection of either the original composition of the cuticle, or the composition of the surrounding phosphate-rich waters. Dissolution of the cuticle and reprecipitation of francolite would have destroyed much of the ultrastructural detail of the cuticle if the francolite was formed primarily by replacement. It is considered, therefore, that the composition of the cuticular francolite in some way reflects the original cuticular composition of the crustaceans.

4.1.3 Process of Phosphatisation.

The preservation potential of materials in a phosphate-rich environment was aptly demonstrated by an excavation of a 155 year old burial in guano which produced a fairly well preserved Dutchman (Watson 1930). Guano has also

preserved textiles and birds for several centuries on Guañape Island (Hutchinson 1950).

Secondary phosphatisation of fossil material appears to produce a consistent microscopic morphology suggesting that the basic processes behind diagenetic phosphatisation may also be similar. Microspherical aggregates of phosphates within the cuticle of *Tealliocaris* are similar to those seen in other phosphatised fossil organisms. The texture of the apatite surfaces of an Early Cambrian invertebrate *Hyolithellus* and of the connecting rings of the Ordovician nautiloid *Bactroceras*, for example, exhibit a very similar microspherical structure (Hewitt and Stait 1985). The phosphates of the Cretaceous fish of the Santana Formation (Martill 1988), and the Jurassic Oxford Clay squid (Allison 1988b) also form microspherular crystal aggregates.

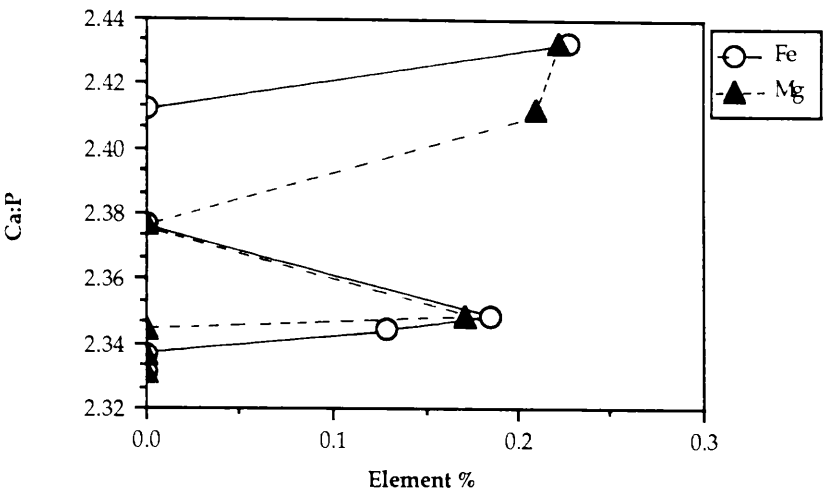
The microspherical structure of the apatite is thought to be related to bacterial activity (Prévôt and Lucas 1986), the pseudomorphic replacement of carbonate by phosphate being initiated by bacteria in a solution of RNA, and being capable of preserving microstructural frameworks in shell or carapace materials. The bacteria are also microspherical, are of the order of 2μm or more in diameter and have been shown to be responsible for the apatite replacement in the Moroccan phosphorite of the Eastern Ganntour Basin (Prévôt and Lucas 1986). Phosphates can also replace tissues and organs as seen in the muscle tissue of the Cretaceous fish of the Santana Formation (Martill 1988) and also in a specimen of *Palaemysis* (Plate 5·7b) and *Tealliocaris* (Plate 5·4a). The specimen of *Palaemysis* has blood vessels, gills, muscle blocks and the gut preserved by phosphates. Most of the soft tissues have been extruded from the body cavity and are disarticulated suggesting at least partial decomposition. The specimen of *Tealliocaris* has muscle blocks preserved *in situ* indicating that phosphatisation occurred very soon after death. Sulphate-reduction causes almost total decomposition of both heavily and poorly calcified crustaceans under anaerobic marine conditions within 25 weeks, and the corresponding rate of methanogenic decay of chitin in freshwater is only slightly slower (Allison 1988a). The state of preservation of the crustaceans in the Manse Burn Formation suggests that the phosphatisation occurred within the first two

weeks after death, as most of the limbs and arthrodial membranes are still intact.

The exocuticle of *Tealliocaris* was phosphatised by rapid diffusion and substitution of phosphates from the water column. This can be seen on a traverse of the exocuticle which shows a gradual increase in the Ca:P values from the outer exocuticle inwards (Fig. 4.3), similar to that found in the phosphate replacement of calcite nodules (Bushinski 1935). A low pH value in the water surrounding the outer cuticle will cause this substitution to occur. The substitution by the phosphate ions appears to have been predominantly of carbonate ions as the sulphate concentration does not change significantly throughout the exocuticle. Sulphate reduction appears to have only affected the outer exocuticle, as the inner exocuticle was probably buffered by a carbonate rich solution due to the decay of the endocuticle. The decaying endocuticle has produced radially crystalline aggregates of calcite, in the form of microconcretions, with low phosphate concentrations, perhaps due to the action of chitinolytic bacteria which commonly cause decay of the crustacean cuticle (Herwig *et al.* 1988).

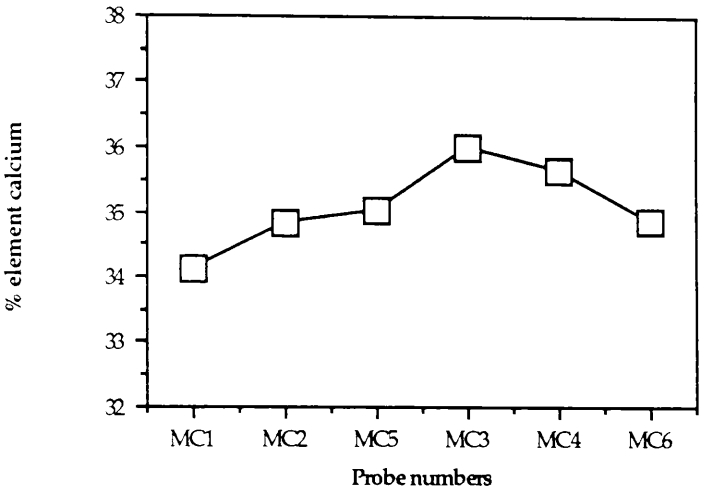
Post-burial pore fluids rich in magnesium and iron, may have caused substitution of the calcium in the outer and inner margins of the exocuticle but did not pervade the entire exocuticle of *Tealliocaris* (Fig. 4.5). This variation of iron and magnesium may also be a reflection of the original variations in the chemistry of the cuticle, rather than as a result of pore fluid effects.

Figure 4.5 Distribution of iron and magnesium through the cuticle of *Tealliocaris*.



A Recent crustacean (amorphous calcium carbonate), a bivalve (aragonitic), and a calcite rhomb were placed in concentrated phosphate solutions to assess the effect of purely chemical phosphatisation on different forms of calcium carbonate (see Plate 4.1). The bivalve, *Donax vittatus*, produced hexagonal laths of apatite (≈100μm in diameter), while the surface of the calcite rhomb reacted to produce large spherical masses of feathery phosphate (≈100μm). The cuticle of the Recent crustacean *Cancer*, used because it lacked phosphates in the cuticle, did not change its basic form for over a year of being exposed to the solution, although colour disappeared after a few hours of immersion. The cuticle formed microspherical aggregates of phosphate (<20μm) similar to those produced in the fossil crustaceans. The actual size of these microspherical nodules may depend on the length of time exposed to the phosphate solution and on the concentration of the solution used. Sections of both unphosphatised and phosphatised cuticle were made from the claw of *Cancer*. The sections, which were analysed using an EDS probe, showed that there were some small changes in the chemistry of the cuticle taking place during phosphatisation. The unphosphatised cuticle of *Cancer* had an average of 35.1% calcium with a slight peak in the middle of the exocuticle (Fig. 4.6).

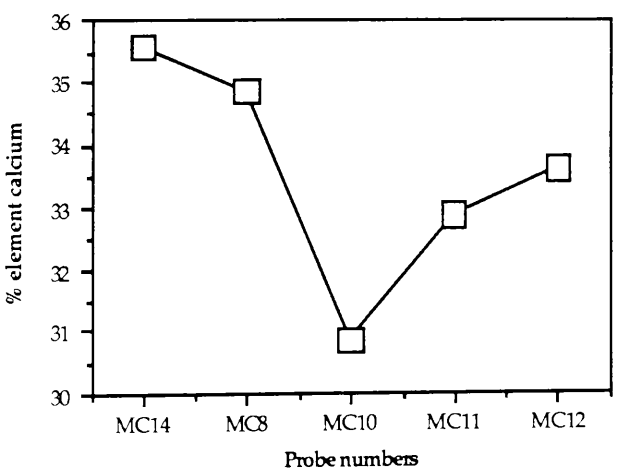
Figure 4.6 Distribution of calcium across the cuticle of *Cancer* (unphosphatised).



(MC1 and MC2=epicuticle; MC5, MC3, MC4, MC6=exocuticle)

In the phosphatised cuticle the calcium concentration is slightly lower in the exocuticle (=32.4%). The epicuticle of the phosphatised sample (Fig. 4.7), however, is much the same as in the unphosphatised sample (=35.2%) (Fig. 4.6).

Figure 4.7 Distribution of calcium across the cuticle of *Cancer* (phosphatised).

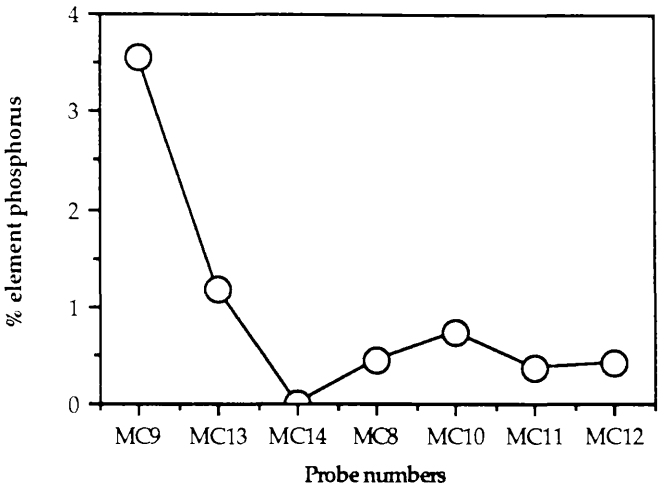


(MC8 and MC14=epicuticle; MC10, MC11, MC12=exocuticle)

The phosphate concentration is higher in the tegumental ducts and it is likely

that this is the route taken by the phosphates in the fossil crustaceans (Fig. 4.8).

Figure 4.8 Distribution of phosphorus through the phosphatised cuticle of *Cancer*.



(MC9 and MC13 are analyses of tegumental ducts in the epicuticle)

Chlorine, sulphur, and sodium decrease in concentration across the exocuticle of both the phosphatised (Fig. 4.9) and unphosphatised samples (Fig. 4.10).

Figure 4.9 Distribution of sulphur, chlorine, and sodium across the unphosphatised cuticle of *Cancer*.

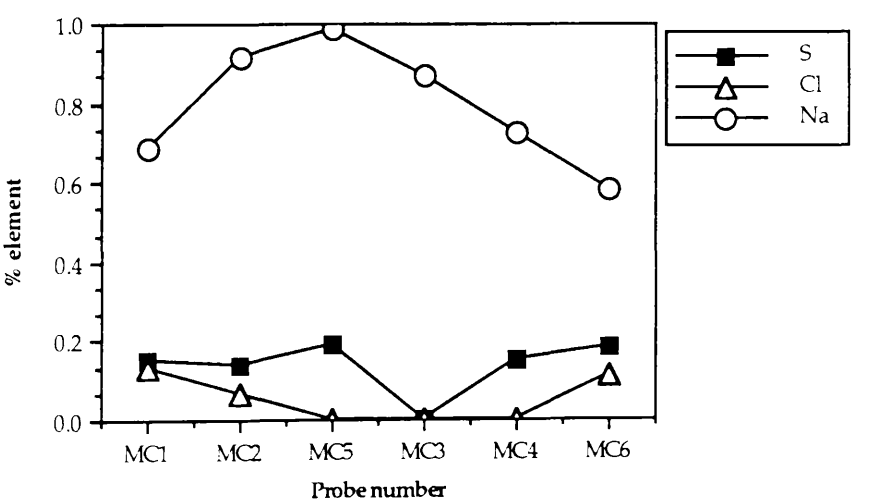
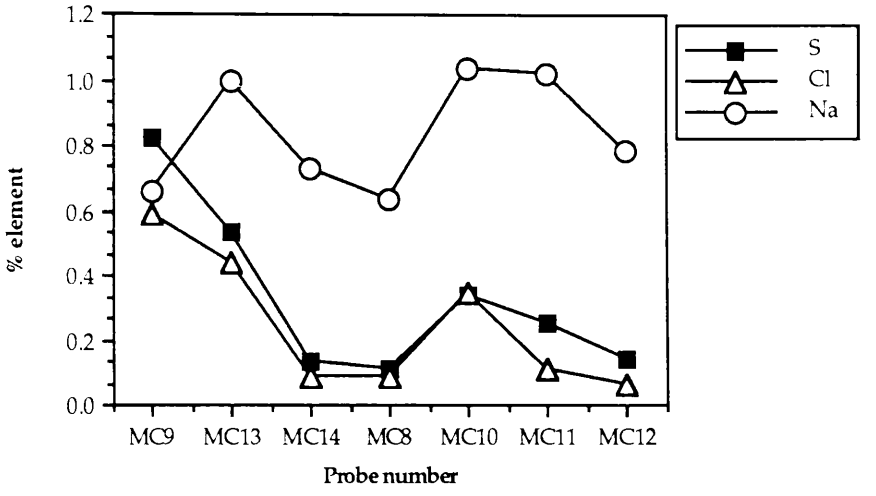
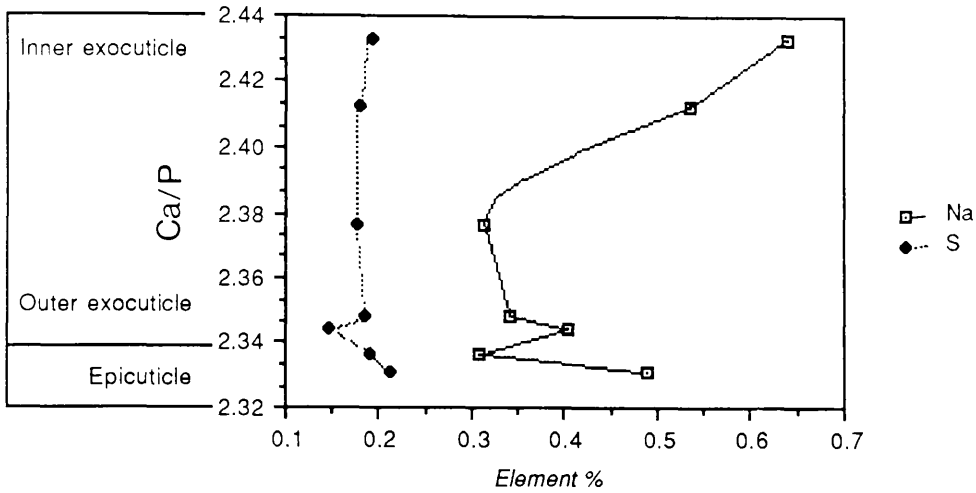


Figure 4.10 Distribution of sulphur, chlorine, and sodium across the phosphatised cuticle of *Cancer*.



The slight variations in the concentrations of the major elements in the cuticle may be as a result of sample bias. The presence of these elements in the Recent crustacean in similar concentrations before and after phosphatisation suggests that the concentrations of these elements in the fossil specimens are close to the concentration in the living animal. The cuticle of *Tealliocaris* has an average calcium concentration (=34.5%) very similar to that of the unphosphatised cuticle of *Cancer*. This concentration is thought to be approximately that of the original living cuticle of *Tealliocaris*.

Figure 4.11 Distribution of sodium and sulphur through the cuticle of *Tealliocaris*.



Pore canals were too small to allow reliable readings of their phosphate concentration to be taken but may have been partly responsible, in conjunction with the tegumental ducts, for the transport of phosphates into the cuticle. The sodium levels (Fig. 4.11) in the cuticle of the fossil crustaceans may give an indication of the life environment of the crustacean, or the environment of phosphatisation of the cuticle (see Chapter 6) depending on whether the concentration of sodium is original or secondary substitution (see section 4.1.2).

4.1.4 Environmental conditions necessary for phosphatisation.

Phosphate is an important element in the life cycle of all living organisms and is found in deoxyribonucleic acid (DNA), ribonucleic acid (RNA), adenosine tri-, di-, and mono-phosphate (ATP, ADP, AMP). In water systems phosphate ions are quickly used by plants and phytoplankton. Eutrophication may occur where phosphates are abundant by blooms of blue-green algae and other nitrogen-fixing organisms. Phosphates are released into the water column from the sediment surface only during anoxic bottom water conditions (Pierrou 1976) due to the decomposition of organic matter. The resulting low oxygen conditions created by phosphate enrichment will eliminate the more sensitive life forms. Freshwater ecosystems are particularily sensitive to increases in phosphate concentration, whereas coastal waters are only affected when exchange with

the marine environment is impeded, causing estuarine circulation. Estuarine environments tend to accumulate phosphates and also to develop anoxic bottom water conditions (Pierrou 1976).

Several experiments and observations on phosphatisation of calcareous materials have provided certain constraints. Fallot *et al.* (1983) found that a decrease in the concentration of HCO_3^-, PO_4^{3-}, SO_4^{2-}, Cl^-, Ca^{2+}, Mg^+, and Na^+ occurred when non-saline mineral water is passed over calcium carbonate granules. The PO_4^{3-} and SO_4^{2-} ion concentrations become negligible, presumably precipitating as apatite. Phosphates (NaH_2PO_4) injected into water saturated in calcium carbonate causes a decrease in the pH and an increase in the conductivity of the water. As much as 90% of the phosphate ions are either fixed or precipitated. The phosphate ion appears to replace the carbonate ions in the calcium carbonate to some extent. An influx of distilled water causes more phosphate ions to precipitate. The precipitation of phosphate minerals can occur in the absence of bacterial or algal activity under experimental conditions (Fallot *et al.* 1983) and hence should occur under natural conditions where phosphate ions come into contact with calcium ions or calcium carbonate. It is more likely, however, that the replacement of carbonate by phosphate is as a result of a combination of biological and chemical processes in nature.

Non-photosynthetic filamentous bacteria are thought to be responsible for phosphate cements in Miocene sediments of the Monterey Formation, California (Williams and Reimers 1983). The bacteria have adapted to a microaeorophilic environment between the oxic layers above and the sulphidic layers below in which they would die during burial. A common constituent of bacteria, carbonic anhydrase (Veitch and Blakenship 1963), may have catalysed the post-mortem precipitation of carbonate-hydroxyapatite (McConnell *et al.* 1961, Smith 1987).

A recently described Cretaceous fish fauna from the Santana Formation of Brazil (Martill 1988) shows phosphatisation of soft tissue. As with many environments where phosphatisation has taken place, the environmental

conditions are much in dispute ranging from brackish to hypersaline. Martill suggests that a mass mortality of nectonic organisms may have occurred due to an occasional influx of hypersaline waters resulting in a restricted benthic fauna. The phosphate occurs in enterospirae, replacing soft tissue, and as a surface coating to bones. The timing of the phosphatisation is interpreted as being prior to burial as no sediment has invaded the body cavity or tissues and there is sometimes a partial disarticulation of the fish. Low oxygen levels at this time, represented by dark organic-rich laminations, would have prevented scavanging and enhanced the preservation potential of the fish. Organic rich laminae may be an indication of widespread prokaryotic mats which survive due to the lack of grazing. The phosphates may have originated from the microbial decomposition of organic material concentrating in the near substrate surface pore waters. It is unlikely that the amount of phosphates released from an individual carcass alone could have caused the phosphatisation of that carcass.

It is suggested that very similar conditions prevailed at the time of the phosphatisation of the crustaceans of the Manse Burn Formation although it is unnecessary to invoke mass mortalities. The decay of algae producing the darker laminations (see Plate 4.2d) would liberate sufficient phosphate to allow the phosphatisation of the crustaceans. The phosphates, taken-up by the algae, may have originated from the weathering of the volcanic rocks, and from hot springs which may have been active in the Bathgate area during the Lower Limestone Group (Muir and Walton 1957), and subsequently concentrated on the substrate surface by the decomposition of the algae. The sediment does not appear to have invaded the body cavities or soft tissues of the crustaceans, and minimal disarticulation of the carcasses suggests that the phosphatisation took place prior to burial in a low energy anoxic environment. The lack of scavanging by benthic organisms, such as ostracodes, also indicates anoxic bottom conditions. There is no evidence to suggest that hypersalinity was the cause of the phosphatisation. It is probably more correct to infer a nutrient-rich freshwater source causing algal blooms and eutrophication. Between these toxic events oxygen levels were high enough to allow shallow bioturbation of the sediment. The low current activity is exemplified by the numerous specimens

where fragile limbs are still found to be attached to the limb bases and in close association with the other parts of the exuviae or carcasses.

4.1.5 Preservation potential of crustaceans.

Decomposition in the marine environment occurs more rapidly than in the terrestrial environment, and a combination of a vulnerable amorphous carbonate cuticle (Prenant 1927) together with chemical and biochemical degradation ensures that crustaceans generally have a low preservation potential. Bacterial activity, for example, can completely destroy marine copepods within 3-11 days depending on water temperature (Harding 1973), and chitinolytic bacteria have been shown to degrade chitin in krill exuviae at a rate of 207 mg/day per gram in a Virginian estuary (Herwig *et al.* 1988). Purely chemical activity, the decalcification of calcareous arthropod remains, has been shown by Aller (1982) to occur near the sediment surface where the pore waters are under saturated in carbonate.

The preservation potential of crustaceans is affected by the depth of burial, degree of oxygenation of the sediment, the degree of bioturbation of the sediment, scavanging, bacterial and chemical degradation, and the degree of physical disturbance (Plotnick 1986, Allison 1988a). The potential for preservation is increased if the effect of the above factors is decreased or stopped completely during the early taphonomic stages. The phosphatisation of the crustaceans, from the Shrimp Member, must have occurred quite rapidly in an environment where most of these factors, such as scavanging, bioturbation, and physical disturbance, did not apply.

4.2 Coprolites and enterospirae.

There are a variety of different types of coprolites and enterospirae found from the Shrimp Member of the Manse Burn Formation. Many have an internal spiral structure with varying degrees of internal collapse and nodule formation (the fossil content of the coprolites and enterospirae is discussed in chapter 6). The enterospirae have undergone a series of early diagenetic porewater

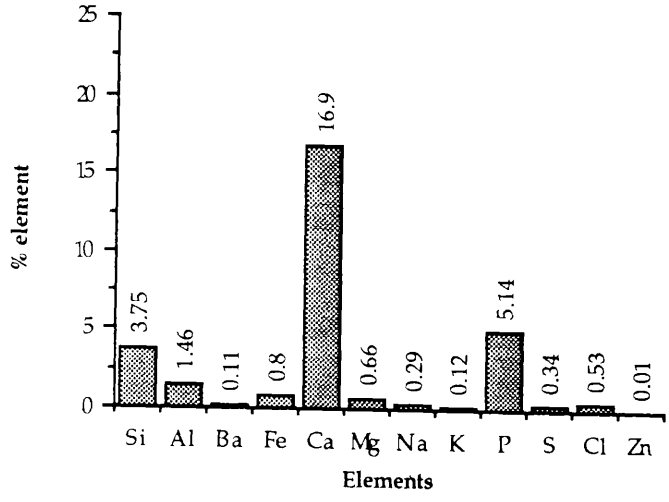
crystallisations most of which are probably related to the decay of the soft tissues. Depending on the extent of internal collapse of the enterospire and the original composition of the decomposing fluids, several stages of porefluid crystallisations can be recognised.

4.2.1 Preservation and diagenesis.

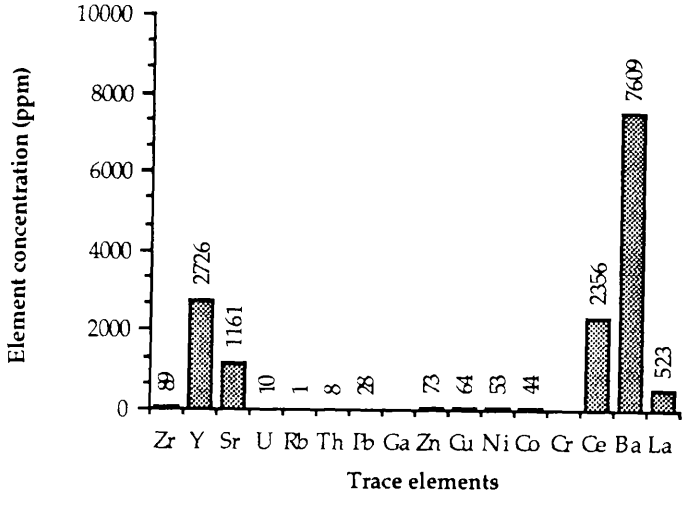
Hutchinson (1950) described a number of processes by which soluble phosphates become more stable. Many minerals present in guano may also have been common to enterospirae and coprolites. Taylorite (a potassium ammonium sulphate), gypsum, stercorite [$NaH(NH_4)PO_4.4H_2O$], brushite [$Ca_{10}(P_2O_8)_3(OH)_2$], monetite [$CaHPO_4$], and hydroxylapatite [$Ca_{10}(P_2O_8)_3(OH)_2$] occur abundantly in guano. Brushite forms at 25°C and below pH6.4 and is found as an encruster on bones in recent deposits. Water extracts phosphates from brushite and monetite as it passes through excreta producing the more stable hydroxylapatite in the remaining excrement. The phosphatic nodules surrounding the collapsed or partially collapsed enterospirae from Bearsden may have formed by the diffusion of such soluble phosphates into a calcium rich environment promoting the precipitation of francolite.

Figure 4.12 Average enterospire ground-mass composition; a) major elements, b) trace element concentration of C1, c) trace element concentration of C2 (see Appendix A30).

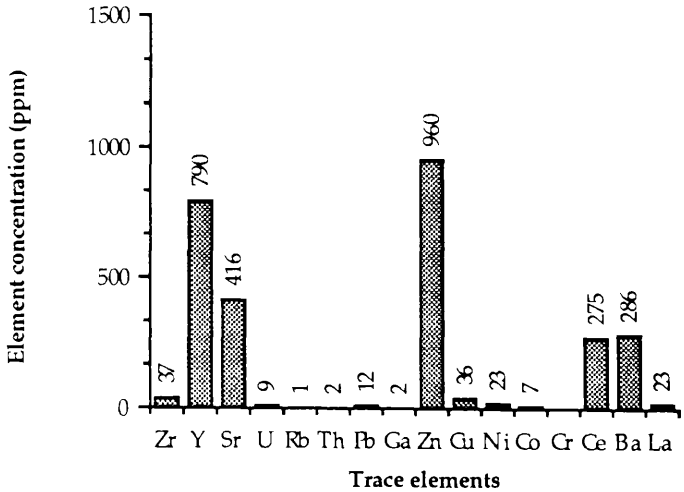
a)



b)



c)



The trace elements in the enterospirae may give an indication of diet and can vary greatly between different specimens. In figure 4.12b/c, enterospire C1 did not contain any fish debris and enterospire C2 contained abundant fish debris.

In most enterospirae the first stage of crystallisation is the formation of phosphate followed by the development of pyrite throughout the enterospire in the form of small individual tetrahedra or by replacement or coating of shelly materials. Pyrite also occurs along the thin lining of the spiral and replacing plant fragments. Sphalerite is a common sulphide within the enterospirae and is associated with a post-collapse crystallisation as it can be seen forming between fractured fish scales. Baryte is not common to all the enterospirae and may be related to a secondary replacement of a pre-existing early sulphate. Most of the baryte has probably entered the enterospirae from secondary pore waters as it does not occur within the early diagenetic nodules (see section 3.3.1). The other porewater minerals which occur in various concentrations and compositions are clays, quartz, calcite and phosphate.

There are several different cement morphotypes which can be distinguished in thin section in transmitted and reflected light as well as by cathodoluminescence (CL) (Table 4.4). These cements can also be distinguished by composition using probe analyses. The interrelationship of these various

cements also gives a relative history of diagenetic processes which affect the enterospirae:-

1) Phosphate genesis within the enterospirae related to decay of the soft tissue and gut contents;

2) Formation of pyrite in the anoxic microenvironment of the enterospire. The pyrite forms euhedral crystals and coats and replaces some of the fossil elements;

3) a) Radially crystallising carbonates within the central collapsed area (orange under CL). This includes the cement which occurs along the lining of the enterospire spiral;

b) Sphalerite also crystallises in some enterospirae soon after collapse and mostly occurs in the outer edges although some occurs internally where collapse has been particular ly severe (NCA3). It also partially fills some bivalves in NCA1;

c) Nodules form mainly around those enterospirae which have undergone a certain amount of collapse causing the diffusion of phosphates into the sediment;

4) The lighter clear carbonate, quartz, clay cement infills bivalves and spaces (dark red in CL). The crystal angles can be seen where the cement has not totally filled the pores;

5) a) Grainy kaolinite fills the central collapse area and other internal collapse areas (blue under CL);

b) This also fills some bivalves in sample NCA1;

c) Compaction of the enterospirae in nodules produces veinlets which are filled with this cement as well as containing fragmentary fish scales indicating forceful injection of the cement;

d) In some enterospirae erosion has taken place while the enterospire was unconsolidated (NCC1);

6) A brown siliceous cement fills spaces in the bivalves;

7) The baryte is probably the last cement to enter the system and may replace previous cements. It can occur abundantly (a) or in trace amounts (b);

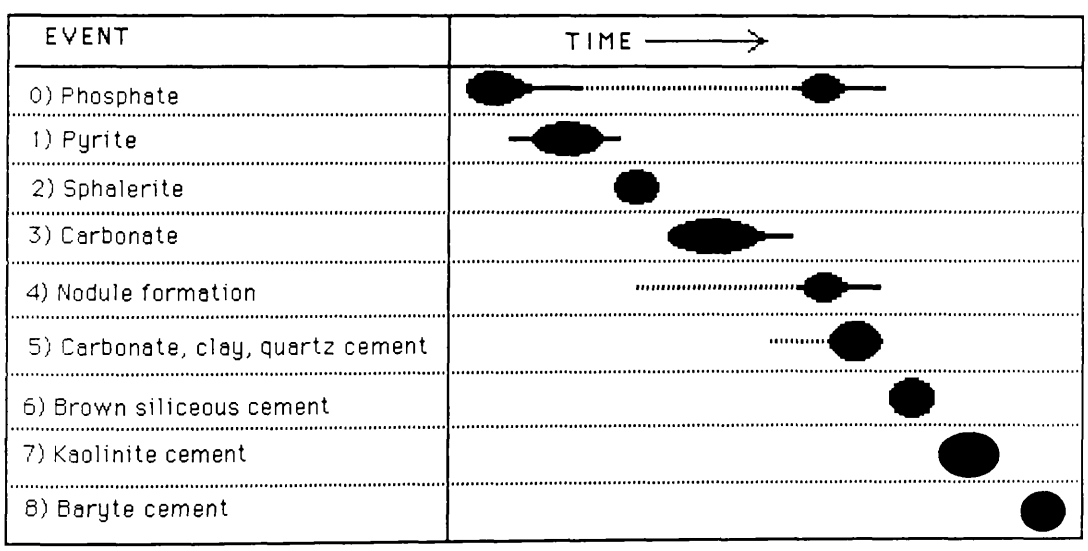
Table 4.4 The phases of diagenetic cements present in a number of thin sections of enterospirae from the Manse Burn Formation.

Sample	Diagenetic stages present						
	1	2	3	4	5	6	7
NCA1	√	√	a	√	a,b	√	b
NCA2	√	√	a	-	a	√	a
NCA3	√	-	a,b,c	-	a,c	-	-
NCA4	√	-	a,b,c	-	a,c	-	-
NCB1	√	√	a	√	a	√	b
NCB2	√	√	a	-	a	-	b
NCB3	√	-	a,b,c	√	a,c	-	b
NCC1	√	-	a,b	√	a,d	-	b
NCC2	√	√	a	√	a	√	b
NCC3	√	√	a	√	a,d	√	b

(√ = present; - = not present)

The timing of the formation of the various cements is sometimes difficult to assess due to the sections not showing the relationships between the cements (Table 4.4). However, sufficient detail has been seen to allow an attempt at defining the diagenetic history of the enterospirae (Table 4.5).

Table 4.5 Proposed diagenetic history of enterospirae from the Manse Burn Formation.



Expanded dark areas represent the most likely relative timing of cementation and crystallisation.

The microstructure of the enterospirae, seen using a Scanning Electron Microscope (SEM), resembles the microspherical bacterial concretions described as preserving the soft tissues of fish and crustaceans (section 4.1.3).

The small amphipolar coprolites may be crustacean coprolites and vary greatly in composition. They consist mainly of organic material with some clay minerals, pyrite and carbonates. There is not any obvious internal structure to these coprolites.

4.2.2 Isotopes $\partial 18O$, $\partial 13C$, $87Sr/86Sr$.

One of the enterospirae from Bearsden was analysed for isotopic ratios of $\partial 18O$, $\partial 13C$, and $87Sr/86Sr$. This was done to attempt to identify the environmental conditions of the formation of the phosphates within the enterospire. The secondary diagenetic calcite was removed prior to the analysis of the isotopic ratios. $\partial 18O$ and $\partial 13C$ were measured using the carbonate ions within the francolite structure.

As the enterospire represents the gut-fill of a fish, it is reasonable to assume that the phosphates were precipitated following the decay of organics contained within the enterospire and also from the decomposition of the enveloping soft tissue of the gut wall. The carbonate and phosphate ions within the carbonate apatite would form from the isotopes evolved during organic decay. Any loss of the lighter isotopes would produce more positive values in the residual material. This means that the original isotopic ratio values would have been more negative than that measured.

Phosphates are thought to produce reliable $\partial 18O$ values for the temperature of formation due to being in equilibrium with the surrounding water (Longinelli and Nuti 1973, Savin 1980). The relationship between the oxygen in the carbonate ions in apatites and co-occurring calcite has been derived by Shemesh *et al.* (1988) and shows a high degree of correlation. Where $\partial^{18}O_{cc}$ is the oxygen isotope ratio for calcite and $\partial^{18}O_c$ is the oxygen isotope ratio for the carbonate ions of apatite, the relationship between the co-occurring species is shown by the expression;

$$\partial^{18}O_{cc}=1.02\partial^{18}O_c-0.89$$

and the relationship between $\partial^{18}O_{cc}$ and temperature is given by the equation;

$$100 \ln \alpha_{(cc-w)}=2.78(10^6/T^2)-2.89$$

where $\alpha_{(cc-w)}$ is the fractionation factor between carbonate and water, and T is in degrees kelvin. Combining the two equations above provides us with an equation for calculating the temperature of the formation of the francolite in the cuticle of the fossil crustaceans, or a value of the isotopic ratio of the water of formation;

$$T = \sqrt{\frac{2.78\times10^6}{1.02\,\delta^{18}O_c - \delta^{18}O_w + 2.00}}$$

Assuming that the temperature of the water could be anything between 15°C and 30°C for an equatorial lagoon, the calculated ∂_w for the waters which precipitated the phosphate ranges from -4.3 to -7.7 (Fig. 4.13).

Figure 4.13 Graph showing the relationship between the temperature of formation of the francolite (T°C) and the isotopic ratio of the water (∂w).

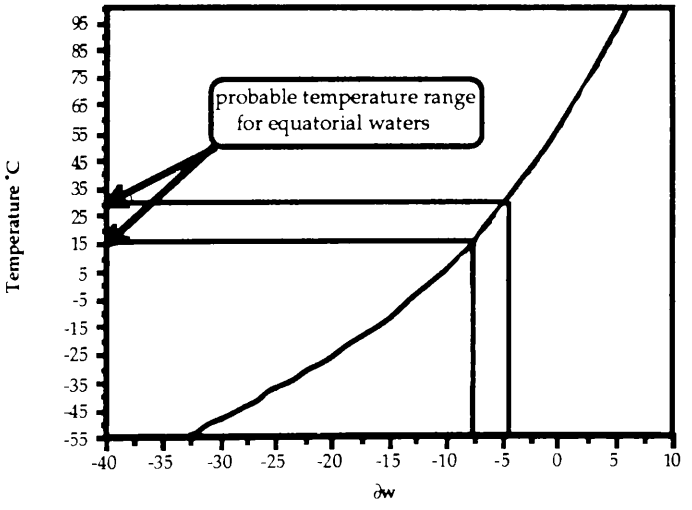


Table 4.6 Isotope ratios of an enterospire from Bearsden.

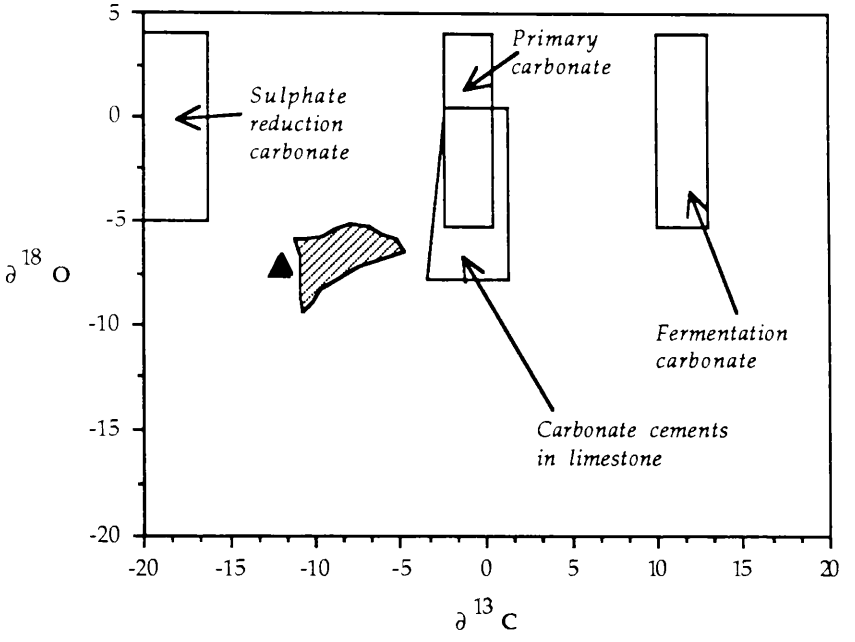
$\partial^{13}C_{PDB}$	$\partial^{18}O_{PDB}$	$\partial^{18}O_{SMOW}$	$^{87}Sr/^{86}Sr$	∂_{wSMOW} (T°C=15/30)
-11.24	-7.22	+23.42	0.70824	-7.58/-4.35
-11.29	-7.32	+23.31		-7.69/-4.46

There is a constant trend in $\partial^{18}O$ values to decrease towards the Precambrian although anomalously low values have been recorded from the Carboniferous (Longinelli 1966, Longinelli and Nuti 1968). The low values recorded for the enterospire are likely to result from the precipitation of phosphates from a meteoric water source.

The $\partial^{13}C$ values will be more positive than the original organic material due to decomposition and loss of some of the lighter isotope. As bacteria make up the bulk of the enterospire, it is likely that they are major contributors to the $\partial^{13}C$ value. The measured $\partial^{13}C$ values fall into the isotopic ratio ranges for eukaryotic algae, cyanobacteria, some anoxygenic photosynthetic bacteria, and methanobacteria (Schidlowski 1988).

Both the $\partial^{13}C$ and the $\partial^{18}O$ values fall close to the range reported for a pellet-bone phosphorite from Israel (McArthur *et al.* 1980) (Fig. 4.14). Although the origin of the phosphate in the Israeli phosphorite is not known, it appears to fall into the field of authigenic phosphate precipitated from non-marine waters.

Figure 4.14 $\partial^{13}C$ and $\partial^{18}O$ data for carbonate fields and some data from McArthur *et al.* (1980, fig. 1). The hatched area represents data from Israel (McArthur *et al.* 1980), and the black triangle represents the data from the Carboniferous enterospire from Bearsden.



The $^{87}Sr/^{86}Sr$ ratio value of the enterospire is similar to previous figures for normal marine carbonates in the Lower Carboniferous (Peterman *et al.* 1970, Burke *et al.* 1982). The strontium ratios probably result from the weathering of a mixture of volcanic rocks ($^{87}Sr/^{86}Sr_v$=0.704), old sialic rocks ($^{87}Sr/^{86}Sr_s$=0.720), and marine carbonates ($^{87}Sr/^{86}Sr_m$=0.708 (approximate value for the Carboniferous)) producing the measured value recorded in the phosphate (Faure 1986). The $^{87}Sr/^{86}Sr$ ratio of sea water (*sw*) is related to the sum of these factors ($^{87}Sr/^{86}Sr_{sw}=0.704_v+0.720_s+0.708_m$) (Faure 1986). A ratio of 60% volcanic source, 20% sialic source, and 20% marine source for the strontium ratios, for example, would produce a combined $^{87}Sr/^{86}Sr$ ratio value of 0.708. It is possible that the $^{87}Sr/^{86}Sr$ ratio is due entirely to the weathering of marine carbonates, however, this is unlikely due to the proximity of active and weathering volcanics within the MVS and the meteoric influence in the precipitation of the phosphates shown by the calculated $\partial^{18}O_w$ ratios.

The strontium isotope ratios suggest that the enterospire phosphates crystallized in an environment which was either normal marine or a mixture of waters dominantly from weathered volcanics, with some old sialic rocks, and marine carbonates. The $\partial^{13}C$ values indicate that the phosphates were formed as a result of bacterial decomposition, and the low $\partial^{18}O_w$ ratios suggest a meteoric influence.

4.3 Calcite preservation.

4.3.1 Myodocopid ostracodes (see Plate 4.2a, b).

The myodocopid ostracodes occur abundantly in the lower part of the shrimp-bearing shales immediately above the marine shales of the THL horizon. The cuticle is preserved as a number of radially crystallised calcite polygonal platelets and microconcretionary nodules. Most of the myodocopids preserve the original outline of the valves but do not preserve the original cuticular ultrastructure. Similar platelets and nodules have been recorded from Recent myodocopid ostracodes resulting from the recrystallisation of amorphous or fine grained calcium carbonate in the cuticle (Sohn and Kornicker 1969).

Fossil myodocopids also preserve these structures. Rolfe (1963, fig 4) figures a specimen of the Ordovician *Elpinella radiata* which has rosette structures. Specimens of the Carboniferous *Eocypridina, Vargula, and Beyrichiana* which were figured by Sohn (1977) also exhibit the rosette platelets. More recently Siveter *et al.* (1987) described similar structures in Silurian and Recent myodocopid cuticles. The morphology of the platelets is thought to depend on the number of nucleation centres perhaps relating to the distribution of pore canals.

All the myodocopid carapaces from the Manse Burn Formation exhibit a similar platelet morphology to 'Case C4' of Siveter *et al.* (1987) which describes the closely packed, perforated rosettes. These may represent pre-moult well-calcified individuals which have undergone post-mortem acicular calcite crystallisation.

Myodocopids from the Viséan 'Granton Shrimp-Bed', near Edinburgh, form platelets corresponding to 'Case D4' of Siveter *et al.* (1987) presumably relating to a different pore canal distribution. The crustacean elements of the faunas present at Granton and the Manse Burn Formation suggest that these represent similar environmental conditions. It may be that the form of the platelets have some limited taxonomic value although it would be necessary to have some cuticular ultrastructure preserved to produce a more precise taxonomic identification.

4.3.2 Eumalacostracans.

Many of the eumalacostracan crustaceans have produced radially crystallised calcite microconcretions (see Plate 4.2c, g). These may have formed by recrystallisation of microcrystalline or amorphous calcium carbonate of the cuticle in a similar manner to the rosettes in the myodocopids (Sohn and Kornicker 1969). Rosettes have been previously recorded in both fossil (Peach 1882; pl 9, fig 4g,h) and modern crustaceans (Peach 1882; p80, Kelly 1901). Dudich (1929) illustrated calcareous nodules formed after soaking a fragment of *Penaeus* in distilled water for 24 days.

The formation of the nodules may be catalysed by chitinolytic bacteria during the decomposition of the cuticle (Herwig *et al.* 1988) prior to any phosphatisation event. Both the microconcretion formation and the phosphatisation affect only the amorphous calcium carbonate of the cuticle. After the formation of crystalline microconcretionary calcite in the crustacean cuticle, phosphatisation can not occur and the converse is also true, the phosphatisation prevents the formation of microconcretions. The endocuticle is the first part of the cuticle to be affected by the bacteria responsible for the microconcretions and in some cases it is possible to have an inner microconcretion preservation of the endocuticle and an outer phosphatisation of the exo- and epicuticle (Specimen A21509b).

Table 4.7 Phosphate concentrations in nodules of fossil crustaceans and the cuticle of some Recent crustaceans.

	Tealliocaris	*Crangopsis*	*Astacus**	*Squilla**	*Cancer*
Ca %	38.06	35.43	30.44	12.25	35.08
P %	0.54	0.41	1.39	1.76	0.00
P/Ca	0.014	0.012	0.046	0.144	-

* taken from Kelly (1901)

Tealliocaris and *Crangopsis* have low phosphate concentrations in the microconcretions relative to the phosphate level in the cuticles of *Astacus* and *Squilla* (Table 4.7). The level of phosphate in the microconcretions is not unusual and may represent the original phosphate concentration in the cuticle of the fossil crustaceans. The greater organic content of the cuticle in *Squilla* corresponds with a lower concentration of calcium relative to phosphate.

Thin sections through altered crustaceans show that the innermost part of the cuticle is most likely to form the microconcretions. This may be due to the phosphatisation front moving from the outer cuticle inwardly not reaching the innermost parts fast enough to prevent the formation of the microconcretions. On lamination surfaces the nodules retain the basic outline of the crustacean but show no segmentation.

Another type of preservation of the crustaceans is by dissolution of the cuticle after burial and infilling of the resulting pore space by drusy calcite. This process (Bathurst 1964) also affects some bivalves. The result is a good external mould of the shrimp which shows the segmentation and surface texture of the shrimp without any cuticular structure within the calcite.

4.3.3 Bivalves.

The bivalve spat from the Manse Burn Formation are mostly decalcified except within diagenetic nodules and enterospirae. The surface ribbing is well preserved on the external moulds and the shells appear uncompacted. Only one of the valves is ever seen except where the shells have been preserved in their entirety in nodules and enterospirae. In large bivalves, such as *Naiadites*, the

pore space left by decalcification has been filled by later drusy calcite. The drusy calcite may have precipitated from calcium carbonate rich pore waters resulting from the decalcification of the abundant bivalve spat.

4.4 Pyrite preservation.

One specimen of *Tealliocaris* and several specimens of the syncarid (*Minicaris*) have been replaced by pyrite due to bacterial decomposition in a highly reducing environment. The crustaceans were presumably brought below the oxic-anoxic transition zone, before decomposition of the cuticle and phosphatisation was complete, by a raising of the level of the boundary relative to the shrimp. This may have occurred while the crustaceans were still exposed on the substrate surface or after shallow burial. The pyrite may have coated the crustaceans during anaerobic sulphate-reducing conditions in the marine environment which results in the formation of an iron monosulphide skin on the surface of the cuticle (Allison 1988a). The anaerobic conditions may form around the decaying shrimp despite aerobic water conditions but the existence of sulphate reducing bacteria is a good indicator of marine conditions (Allison 1988a).

Leiopteria is also preserved in pyrite. This may be due to a different shell structure, organic content, or mode of life from the other bivalves at this horizon. It is a byssate bivalve which occurs in concentrated masses perhaps attached to an aquatic plant which is no longer preserved. *Leiopteria* is a facultative commensal which is also found attached to the cephalic shield of *Cyclus*. Although *Leiopteria* is pyritised, the cuticle of *Cyclus* is not. This may be due to the amorphous nature of the cuticle of *Cyclus* while *Leiopteria* has an aragonitic shell. The phosphatisation was not strong enough to dissolve the aragonitic shell of *Leiopteria* prior to the anoxic reduction of the shell producing pyrite.

Plate 4.1

a) Highly magnified dissolution of a calcite rhomb by a concentrated phosphate solution (X130).

b) Resulting phosphate morphology crystallized on a calcite rhomb (X130).

c) Phosphate crystallization on a bivalve (*Donax vittatus*) exposed to a concentrated phosphate solution (X130).

d) Phosphate crystallization on a crustacean (*Cancer*) exposed to a concentrated phosphate solution (X130).

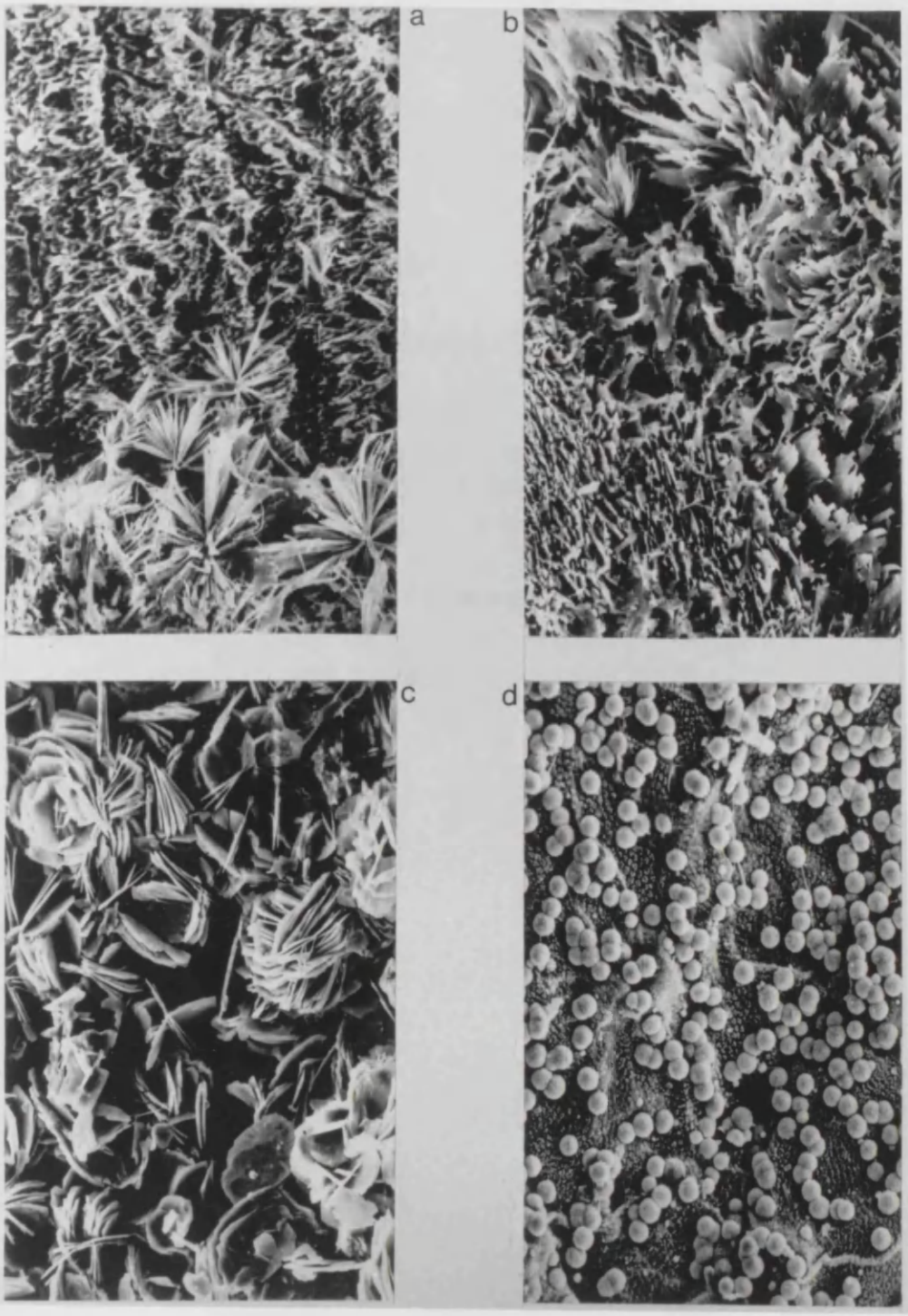

a
b
c
d

Plate 4.2

a) A myodocopid ostracod from the Shrimp Member showing the diagenetic rosette structures of the recrystallized carapace (X15).

b) Enlargement of the rosettes showing the angular nature of the contacts between them (X42.5).

c) Diagenetic crustacean calcite microconcretions from the Shrimp Member (X250).

d) Section through the sediment of the Shrimp Member showing the laminar structure (X35).

e) *Cavusgnathus naviculus* from the Posidonia Member (X70).

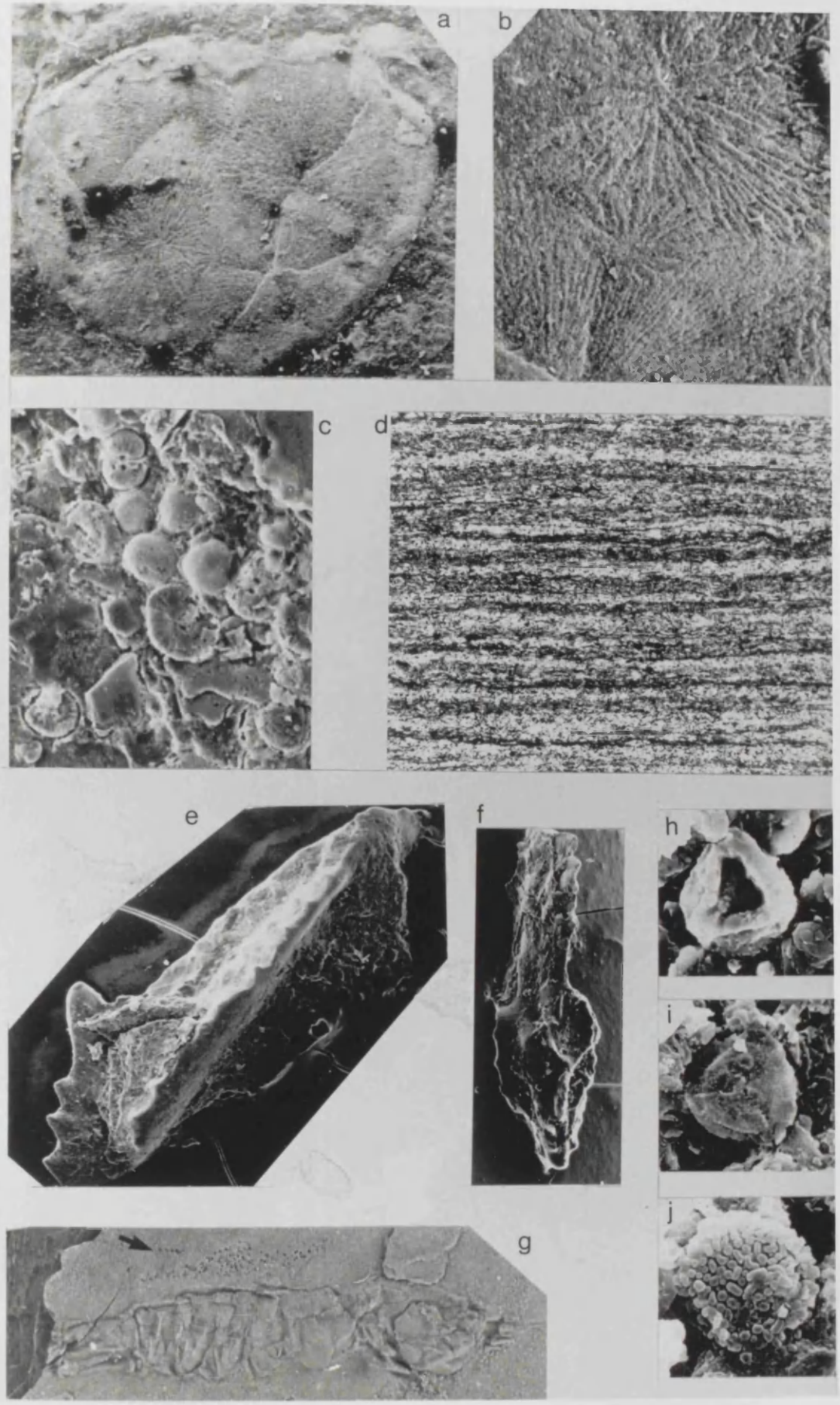
f) *Gnathodus girtyi* from the Posidonia Member (X70).

g) Well preserved *Crangopsis eskdalensis* (phosphatised) alongside decomposed crustacean outlined by calcite microconcretions from the Shrimp Member (X5).

h) *Densospora triangularis* from the Shrimp Member (X700).

i) *Lycospora noctuina* from the Shrimp Member (X700).

j) *Verrucosisporites morulatus* from the Shrimp Member (X700).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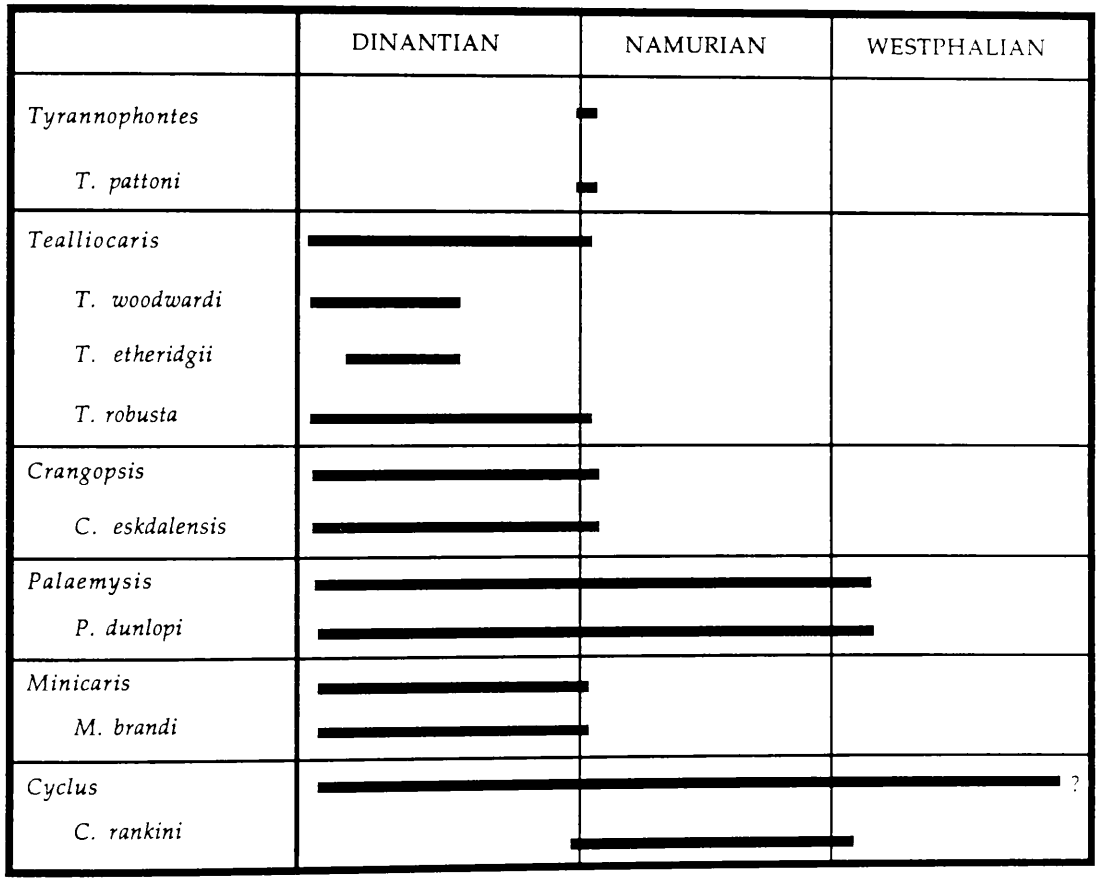
Crustacean Palaeontology of the Manse Burn Formation

Only five species of malacostracan crustaceans are found from the Manse Burn Formation in the western Midland Valley of Scotland. These crustaceans, which include, *Tyrannophontes pattoni*, *Crangopsis eskdalensis*, *Palaemysis dunlopi*, *Tealliocaris robusta*, and *Minicaris brandi*, are described in terms of their relationships with extant crustaceans and other fossil groups of the same age. One maxillipod of the Subclass Copepoda, *Cyclus rankini.*, is also described, although, its precise position within this subclass is uncertain.

Table 5.1 Stratigraphic distribution of the crustacean genera and species represented in the Manse Burn Formation.



Specimens described or figured here are held in the following repositories (abbreviations in parentheses): Hunterian Museum, Glasgow (HM); Royal Museum of Scotland, Edinburgh (RMS); Zoology Museum, Cambridge University (UCZ); British Geological Survey, Edinburgh (BGS); British Museum of Natural History, London (BM).

5.1 History of research into British Carboniferous fossil crustaceans.

5.1.1 *Tyrannophontes pattoni*(Peach 1908).

In 1882, Peach first described the species *Anthrapalaemon parki*, from the Glencartholm locality, near Langholm, which he described with the Decapoda. A new genus, *Palaesquilla pattoni*, which appeared in the fossil list appended to the paper by Patton and Coutts (1885, p327), and also mentioned by Coutts (1888, p173), was later (Peach 1908, p51) considered to be a *nomen nudum* and was redescribed as *Perimecturus pattoni*.

Peach (1908) erected the Family Perimecturidae to represent a group of crustaceans, intermediate between Lophogastridae and the Anaspidae (Peach 1908, p39), with characters which suggest squillid affinities (Peach 1908, p53). In 1908, Peach renamed *A. parki* as *Perimecturus parki*, and a number of new species and subspecies of this genus were also described (*P. parki duplicicarinatus*, *P. stocki*,.*P. elegans*, *P. communis*, *P. ensifer*, and *P. pattoni*).

In 1962, Brooks established the Order Palaeostomatopoda to include the earliest fossil representatives of the hoplocarid precursors to the stomatopods. Schram (1979) synonymised the species of *Perimecturus* into two, single species, genera and a species of uncertain affinities: *Perimecturus parki*, *Bairdops elegans*,and *'Perimecturus' pattoni*.

The first tyrannophontid species to be described was from the Namurian Bear Gulch Member of Montana (Schram 1969, Factor and Feldmann 1985), *T.*

theridion. This genus was erected by Schram (1969) to include specimens which showed characters intermediate between palaeostomatopods and stomatopods. These characters included the specialization of anterior thoracic limbs into subchelae.

The palaeostomatopod specimens found in the Shrimp Member represent a species of *Tyrannophontes* on the basis of the morphology of the tail fan and the thoracic limbs. Only three specimens are known from the Shrimp Member, but these show enough detail to distinguish them from *Perimecturus* and *Bairdops*. Only two of these specimens were found during the course of this study, one from Bearsden (by Miss S. Aitcheson), and one from the Red Cleugh Burn (by Mr. P. McDonald). The third one was first described by Peach (1908) as *Perimecturus pattoni*.

5.1.2 *Crangopsis eskdalensis* (Peach 1882).

A small crustacean, from the sediments at Ardross, was described by Salter in 1861 (Brown 1861) as resembling *Gampsonyx*, and was named *Uronectes (Gampsonyx) socialis*. In the same year, Salter (1861) redescribed this shrimp as *Palaeocrangon socialis*, recognizing that it was not related to *Uronectes* on the basis of the number of abdominal segments. Salter (1863) found that *Palaeocrangon* was actually a small, previously described, Permian isopod and, therefore, had to rename the new genus, *Crangopsis*. In 1862, Huxley (p421) described a crustacean from a dark shale 36 fathoms (63.5m) above the Hurlet Coal, two miles (≈3.2km) west of Paisley. He believed this shrimp to be a species of *Pygocephalus*, although from his description and sketch, the shrimp is identical to what came to be known as *Crangopsis*. The stratigraphic position of the dark shale, from which it came, is at the approximate horizon of the Shrimp Member of the Manse Burn Formation in the Paisley area (Schram 1979), which is ≈59m above the Hurlet Coal at Fulton, four miles (≈6.4km) west of Paisley (Macnair 1915). Woodward (1868) recognised that this specimen did not represent any known species of *Pygocephalus* and suggested the new name *P. huxleyi*. It was not until Peach (1908) revised the Carboniferous Crustacea that *P. huxleyi* was recognised as a species of *Crangopsis*.

In 1882 and 1883, Peach described two new species of *Crangopsis* which he mistakenly named *Palaeocrangon eskdalensis*, and *P. elegans*. This was later rectified in his monograph of Scottish Carboniferous Crustacea (1908) in which he described several other new species, *C. couttsi*, *C. rhodesi*, *C. magna*, *C. robusta*, *C. minuta*, and *C. hastata*. Peach (1908, p82) differentiated between two groups of *Crangopsis* on the basis of the pleura of the second abdominal somite. On *C. eskdalensis*, *C. socialis*, and *C. huxleyi*, the pleura overlap those of the first and third, whereas, in the others the pleura do not. The latter group were later synonymised with *Anthracophausia* by Brooks (1969). The specimens of *Crangopsis couttsi*, of the group synonymised with *Anthracophausia* (Brooks 1969), were correctly assigned by Peach (1908, p76-78) to the genus *Crangopsis*, and are reinstated as such in this study.

Schram (1979), in a major revision of the Carboniferous crustacean genera, placed *Crangopsis* with the Hoplocarida on the basis of a similarity in the morphology with *Aratidecthes* and *Kallidechthes*. The view that *Crangopsis* represented a hoplocarid was retained by Schram (1986) despite the lack of diagnostic features, such as the triflagellate antennules. The whole Order Aeschronectida needs to be fully revised as both *Crangopsis* and *Palaemysis* lack the triflagellate antennules and have a more mysid-like morphology.

Schram (1979) recognised two species of *Crangopsis* which could be differentiated on the shape of the pleura of the abdominal somites. These two species correspond with two species belonging to the first group of *Crangopsis* morphologies originally described by Peach (1908), *C. eskdalensis* and *C. socialis*. The only specimen of *C. huxleyi* could not be located by Schram (1979, p42), although he suggested that it might represent a specimen of *C. socialis*. On the basis of the original sketch by Huxley (1862, p421), however, it seems more likely that it is more closely allied to *C. eskdalensis*.

Crangopsis socialis and *Waterstonella grantonensis* are very difficult to differentiate between, as almost a complete range of morphologies can be

recognised resulting from preservational differences within the lithology in which they co-occur. A specimen of *Crangopsis* figured by Briggs and Clarkson (1983, plate 22 fig. 7) has the full complement of biramous thoracic limbs also recorded for *Waterstonella*. This, in conjunction with morphometric data, suggests that these two genera should be synonymised.

The species of *Crangopsis* collected from the Manse Burn Formation is likely to be *Crangopsis eskdalensis*.

5.1.3 *Palaemysis dunlopi* Peach 1908.

The generic name, *Palaemysis*, was first used in a list to the fossils found from the Limekilns Quarry and Kirktonholm Mines at East Kilbride (Patton and Coutts 1885, p327). Peach (1908) erected the new genus *Palaemysis* to contain a number of specimens of which only the last few segments of the abdomen and the tail fan were preserved. The tail fan of these specimens were similarly "forked", and Peach (p57) placed them in the same genus with reservations. These specimens were split into several species depending on the relative lengths and widths of the various features of the tail fan. He recognised the three species, *P. dunlopi* (from Greengairs, near Airdrie), *P. couttsi*(from East Kilbride, near Glasgow), and *P. tenuis*(from Glencartholm, near Langholm), and designated *P. dunlopi* as the type species (p60).

Palaemysis was initially described as having affinities with the Mysida (Peach 1908, p57), although, Brooks (1962) decided that the evidence for this was not strong enough, and placed it in the Order Eocarida. Brooks (1962) erected the Order Eocarida to include all fossil genera which have similarities with the Mysida, Euphausiacea, and the Decapoda, but which could not be confidently assigned to any one of these orders. In 1969, Brooks (pR342) synonymised *Palaemysis* with *Anthracophausia* (Schram 1969), along with a number of Peach's (1908) species of *Crangopsis* (*C. couttsi, C. rhodesi, C. magna, C. robusta, C. minuta,* and *C. hastata*). It was not until Wood (1982) discovered complete specimens of a crustacean with the same tail fan as Peach's original genus *Palaemysis*, that a full description of the morphology and taxonomic position could be made.

Despite the presence of complete specimens of *Anthracophausia*, which were figured by Peach (1908, plate 9) and Schram (1979, figs. 26-29), *Palaemysis* continued to be considered a synonym of *Anthracophausia* (Briggs and Clarkson 1983, Clarkson 1985, Schram 1986). *Palaemysis* is, here, reinstated as a separate genus from *Anthracophausia* due to major morphological discrepancies between the two genera. Schram (1986) suggested that *Anthracophausia*, which includes the *Palaemysis* forms, may be related to the Euphausiacea. *Palaemysis*, however, has eight thoracopods, of which the anterior-most limb is much shorter, possibly representing a maxilliped, suggesting affinities more with the Mysida than with the Euphausiacea. As there is some difficulty in relating the fossil genera to extant orders, it is proposed that the Order Eocarida should be preserved to include enigmatic crustaceans which have basic caridoid features, but which cannot be placed into extant orders with confidence.

Aratidecthes, which has been classified as a hoplocarid may, in fact, be synonymous with *Palaemysis* based on the similarity between the figures of *Aratidecthes* produced by Schram (1969, figs. 124-128), *Palaemysis* by Peach (1908, plate 8 figs. 12-14. 16-25), and the specimens described here. Further work will need to be done on the original specimens figured by Schram before this synonymy can be made, as the anterior spinose segmented limb of *Palaemysis* (Wood 1982, Schram 1986) has not yet been recorded on *Aratidecthes*.

The species of *Palaemysis* described here can not be adequately differentiated from the type species, *P. dunlopi*, as the specimens of the *P. dunlopi* are incomplete. The morphology and morphometrics of the tail fan of *P. dunlopi*, however, are similar, and the specimens from the Manse Burn Formation are therefore, identified as being of the same species.

5.1.4 *Tealliocaris robusta* Peach 1908.

Etheridge (1877, p.872) described a species of crustacean allied to the genus *Palaemon* from the Lower Carboniferous near Dunbar and called it

Anthrapalaemon? woodwardi. Etheridge later confirmed this designation in a redescription based on new specimens from new localities near New Castleton, Coldstream, and Duns (Etheridge 1879). In 1882, Peach (p76) described more species of *Anthrapalaemon* from Glencartholm, near Langholm, on which he noticed the pleura of the second abdominal somite overlapping those of the first and third. These specimens, however, including *A. woodwardi*, differ from other anthrapalaemonids which have undifferentiated abdominal somites and a telson with distinct furcal lobes. Basing his analysis on shrimps from other localities, Peach (1908) redescribed *A. woodwardi* and synonymised it, together with similar shrimps (Peach 1882, 1883), with his new genus *Tealliocaris*. Peach identified six species of *Tealliocaris* (*T. loudonensis, T. woodwardi, T. etheridgii, T. robusta, T. formosa* and *T. tarrasiana*), and several subspecies. In 1957, Copeland described further species of *Tealliocaris* from the Upper Carboniferous of Canada which were later assigned to a new genus *Pseudotealliocaris* by Brooks (1962). Following the descriptions by Brooks (1969) of *Pseudotealliocaris*, Schram (1979) assigned the Scottish *T. robusta* and *T. etheridgii* to the species *Pseudotealliocaris etheridgei*. Schram (1979) also synonymised *T. loudonensis* Peach 1908 and *T. tarrasiana* Peach 1908 with *T. woodwardi*. This view was supported by the recent redescription of *T. woodwardi* by Briggs and Clarkson (1985a) who provisionally placed *Tealliocaris* in the Waterstonellidae following the classification of the Eumalacostraca by Schram (1981b). In 1986, Schram placed *Tealliocaris* in the Order Pygocephalomorpha which represents a fossil taxon closely related to both the Mysida and the Lophogastrida.

Wood (1982) initially suggested that the genus represented in the Manse Burn Formation was *Pseudotealliocaris*. As a comparison, specimens of *Tealliocaris* and *Pseudotealliocaris* (*sensu* Schram 1979) were studied in detail, with the result that the species *P. etheridgei* of Schram (1979) is now reassigned to *Tealliocaris*. The species of Peach (1908) subsumed by Schram within *P. etheridgei* become freshly defined species, *T. etheridgii*, and *T. robusta*. *Tealliocaris woodwardi* (*sensu* Schram) is recognised as a valid designation while the Canadian species assigned to *Pseudotealliocaris* by Brooks, and the

overall validity of that genus remain to be investigated.

The present reinterpretation of the morphology of *Tealliocaris*, based on new and more perfectly preserved specimens has allowed the genus to be removed from the Waterstonellidae and allied to the Decapoda, and has thrown doubt upon the validity of Scottish members of the genus *Pseudotealliocaris*. The species of *Tealliocaris* from the Shrimp Member of the Manse Burn Formation is identified as *T. robusta*.

5.1.5 *Minicaris brandi* Schram 1979.

Minicaris brandi is a crustacean which belongs to one of the more interesting crustacean orders, the Syncarida. This order was first described from fossil material 45 years before the discovery of living representatives. It was in 1847 that Jordan described the first syncarid crustacean,*Uronectes fimbriatus*, but it was not until much later that it was recognised as representing a new crustacean taxon by Packard (1885, 1886). Packard named this new taxon, the Syncarida, which was soon added to by other similar fossil crustaceans, such as *Acanthotelson* and *Palaeocaris* (Schram 1986). In 1882, Peach recognised a Scottish syncarid species, *Palaeocaris scotica*, which he described as having undoubted decapod characters. It was not until 1893 that the first living representative of this order, *Anaspides tasmaniae*, was discovered (Thomson 1893). In 1908, Peach described a further species of *Palaeocaris*, *P. landsborough*, and redescribed *P. scotica* in the light of the discovery of *Anaspides tasmaniae*, placing them in the Family Anaspidae. The taxon Syncarida was elevated to the ordinal status in 1904 by Calman, and Brooks (1962) separated the Palaeozoic taxa with his Order Palaeocaridacea. In 1984, the fossil Syncarida underwent another major revision by Schram resulting in three suborders being recognised within the Syncarida, the Bathynellacea, the Palaeocaridacea, and the Anaspidacea. These suborders are still recognised by Schram (1986) and and are used in this thesis for the classification of the syncarid from the Shrimp Member.

The species of syncarid from the Manse Burn Formation was first identified as *?Minicaris sp.* by Wood (1982). The original description of the genus *Minicaris*

was based on a single, poorly preserved, specimen from a bore sample at Long Livingston (Schram 1979). Due to the similarity between the tail fan of the type specimen and those of the specimens from the Shrimp Member, it is likely that they represent the same species. Several new features of this fossil syncarid suggest that it may be closely related to *Squillites spinosus* from the Mississippian of Montana. There are, however, a number of differences which are considered to be generic, and the genus *Minicaris* is, here, retained.

The genus *Squillites* was placed in a separate family from the other Palaeocaridacea due to the distinctive form of the appendages which can be favourably compared with the extant *Anaspides tasmaniae* (Schram and Schram 1974). *Minicaris brandi* is, therefore, removed from the Family Minicarididae, and placed in the Family Squillitidae on the basis of the biramous annulate, and setose, pleopods, the ornamentation of the thoracic tergites, and the presence of a broad rostrum on the cephalon.

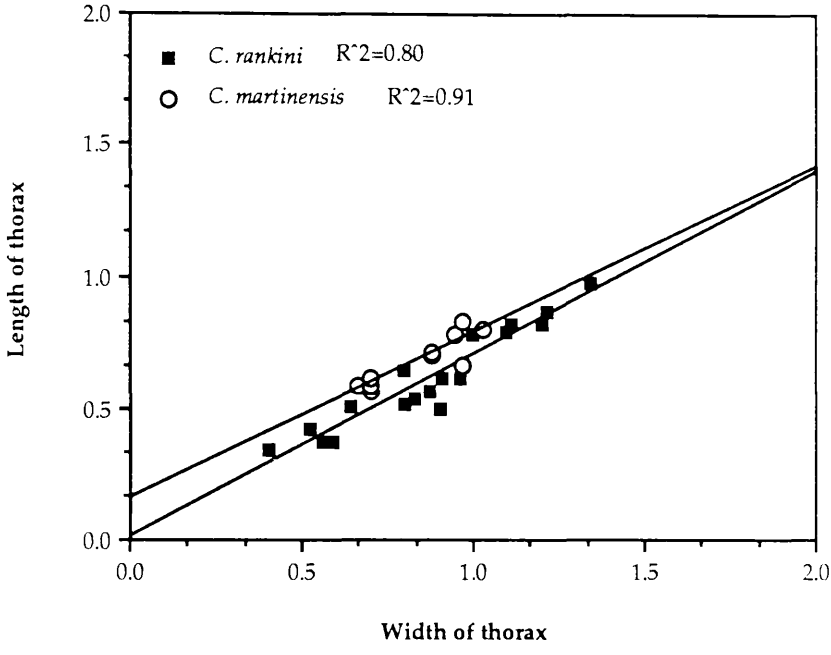
5.1.6 *Cyclus rankini* Woodward 1868.

The genotype of *Cyclus* is *C.radialis*, which was initially described as the species *Agnostus? radialis*(Phillips 1836). In 1842, De Koninck erected the genus *Cyclus* to include *C. radialis* after recognizing that this animal did not represent a species of *Agnostus*. This species is a representative of the convex forms of *Cyclus* which are found in limestones.

The first 'flat' form of *Cyclus*-like arthropods was recognised by Von Meyer (1838), which he named *Limulus agnotus*. This species eventually became known as *Halicyne agnota* by Von Meyer in 1844, and *Cyclus agnota* by Woodward (1870). This species is now the genotype of *Halicyne* (Hopwood 1925). In 1868, Woodward described the first Scottish Carboniferous flattened form of *Cyclus*, *C. rankini*, from Carluke near Glasgow. A second Scottish species from Glencartholm, near Langholm, was later described by Peach (1883), *C. testudo*. Despite the close similarity between the flattened forms of *Cyclus*, and *Halicyne*, they are clearly not of the same genus. *Halicyne* has several significant generic differences, such as the lack of a posterior indentation of the head shield and the lack of anterior subchelate limbs (Gall

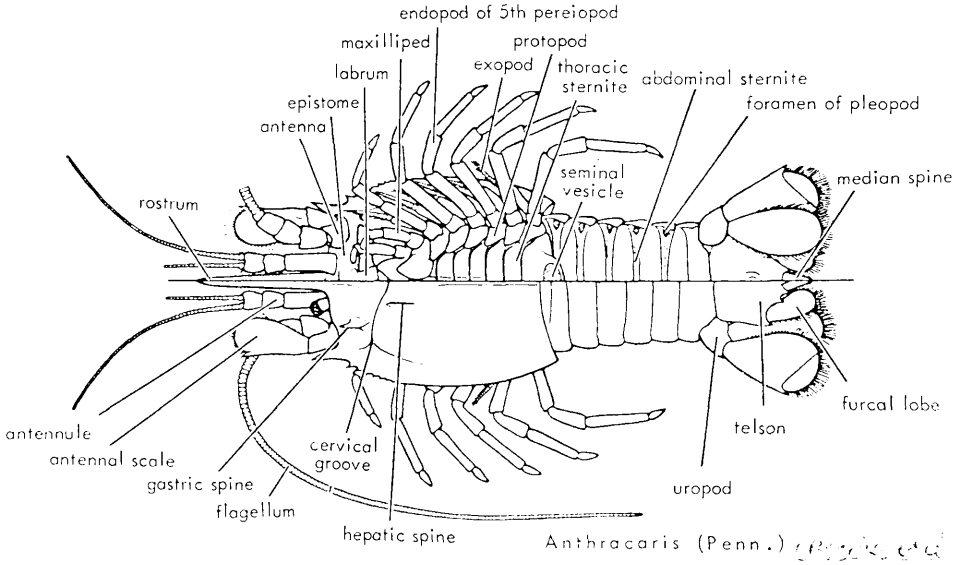
and Grauvogel 1967). Trümpy (1957) suggested that it may be necessary to erect a new genus to contain the flattened forms of *Cyclus*. The differences between the flattened and highly convex forms of *Cyclus* may be due purely to taphonomy. The radial structures seen on the highly convex forms seems to correspond to the radial structures of the flatter forms.

Figure 5.1 The relative proportions of the thorax of a flat form of *Cyclus*, *C. rankini*, and a more convex form, *C. martinensis* Goldring 1967. (measured in mm).



The main differences between the two forms is that the phosphatised flatter forms sometimes preserve the thin head shield and limbs, and are found in compacted shales, whereas, the convex carbonate forms, which are found in limestones, do not. Due to the differences between the preservational environments of these forms, it is suggested that most of the differences identified by previous authors may in fact be taphonomically produced, rather than due to true morphological differences.

The affinities of *Cyclus* have baffled researchers and produced many varied interpretations. Gill (1924) noted that there was a similarity between the



Anthracaris (Penn.)

large sub-chelate limbs of *Cyclus* and those of extant parasitic copepods, but concluded that the radial coxae suggested a xyphosuran relationship, while other workers favoured an affinity with eurypterids. Hopwood (1925) suggested a branchiuran affinity, and also placed the flattened forms of *Cyclus* with *Halicyne*. The similarity between *Cyclus* and branchiurans is, however, only superficial as there are substantial differences.

The specimens of *Cyclus* from the Shrimp Member of the Manse Burn Formation could not be differentiated from *C. rankini* and are thought to be representatives of this species.

5.2 Crustacean Biology.

5.2.1 Anatomy.

Throughout the malacostracans morphologies are broadly similar and can therefore be dealt with generally. There are five cephalic and eight thoracic segments, or somites, which are fused together forming the cephalothorax. This is covered by a carapace in most malacostracans although their are some exceptions, such as the Syncarida.

All the thoracic somites have paired appendages. Attached to the anterior-most, or cephalic somites, are the antennae, the antennules, the mandibles, the first maxillae, and the second maxillae respectively. The eight thoracic somites also bear paired appendages, pereiopods or thoracopods, which can be variably modified to perform particular functions, such as in the Decapoda where the first three pereiopods, or maxillipeds, are modified to aid in the manipulation of food in front of the mouth parts. All appendages consist of an inner branch, the endopod, and an outer branch, the exopod. Groups can be differentiated initially on the basis of the number of maxillipeds (eg: Syncarida = no maxillipeds; Mysidacea = one to two maxillipeds; Decapoda = three maxillipeds (Moore and McCormick 1969)), although this is more difficult in fossil material. The posterior six somites of the body constitute the abdomen, five of which bear paired biramous appendages, the pleopods. The

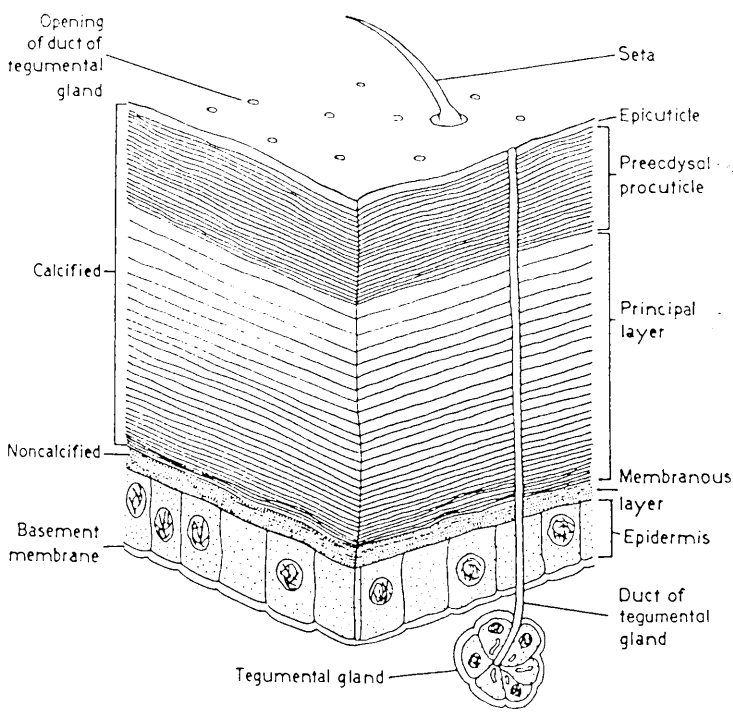
tail fan, which consists of a pair of biramous plates, the uropods, and the telson, is attached to the sixth somite.

The body of crustaceans has many sites for chemo- and mechano-reception. The antennules are thought to be chemoreceptive over a distance from the animal (Phillips *et al.* 1980), while the receptors in the mouth parts and legs respond on contact. Mechanoreceptors help in the determination of vibration, limb position, and gravitational forces. They are positioned over most of the cuticle so as to respond to water currents or other stimuli.

In lobsters, the nervous system consists of an anterior cerebral ganglion that lies above the oesophagus, and is connected to the thoracic and abdominal trunk nerve by a pair of circum-oesophageal commissures. The chain of ganglia may be either elongated or concentrated. Two pairs of giant fibres, lateral and medial, run the length of the abdomen.

The circulatory system consists of a muscular heart, thin-walled arteries that carry blood away from the heart, and a series of irregular channels developed from the primary body cavity which carry the blood back to the heart. Not all crustaceans have hearts, however, and circulation, in this case, is provided by body movement or muscular and gut contractions (McLaughlin 1982). The arteries eventually branch into much smaller vessels that open into tissue spaces. Posteriorly, the artery divides into the sternal artery and the posterior abdominal artery. The ventral abdominal artery supplies the abdominal musculature and some of the pleopods. In the mysidaceans there are lateral arteries and a posterior artery which extend into the abdomen. The sternal artery branches out to the pereiopods and mouth parts. The abdominal artery supplies much of the abdominal musculature, appendages and the intestine. The somatic muscle fibres of crustaceans resemble those of vertebrates in that they are multinucleated and striated.

Most crustaceans respire by forcing water through the branchial cavity by the action of scaphognathites of the second maxillae. Some crustaceans, such as the Syncarida, have a simple epipodal gills. In the Stomatopoda the pleopods act



A generalized view of the crustacean cuticle.

as the primary respiratory structures. Water enters the cavity from the posterior margin of the carapace and between the coxae of the pereiopods, and exits anteriorly. Gills extend into the branchial cavity from the maxillipeds and pereiopods in most malacostracan groups. In environments of variable oxygen concentrations the crustaceans are able to regulate heart beat correspondingly and can therefore tolerate a wide range of concentrations.

Digestion in crustaceans is aided by the thick chitinous lining in the cardiac section of the foregut that is calcified in certain sections to form the gastric mill. Feeding in crustaceans is varied, and they have adapted to perform a number of feeding modes. These include deposit feeding and scavenging, grazing, predation, parasitism, and filter feeding. Crustaceans do not adhere rigidly to any one category but may employ more than one feeding mechanism without having any particular structures, or behaviour pattern, usually associated with that mode of feeding. The crayfish, *Orconectes immunis*,for example, supplements its, normally carnivorous mode by filter feeding, especially after ecdysis when it is less well protected from the environment (Grahame 1982).

5.2.2 The cuticle.

Three major subdivisions of the cuticle are recognised 1) the epicuticle - the thin outermost layer; 2) the exocuticle - also known as the preecdysial procuticle; 3) and the endocuticle - also known as the postecdysial procuticle. Reabsorbtion of the endocuticle occurs during premoult. The cuticular exuviae consists of the exocuticle and the epicuticle.

The epicuticle may consist of more than two layers and the surface may show the outlines of the epidermal cells that secreted it (Drach 1939). On some thin cuticles, such as in a parasitic copepod and a cladoceran, no epicuticle is visible (Stevenson 1980). Calcium salt crystal aggregates occur in the epicuticle in flat radiating plaques and in vertical columns.

The procuticle appears to consist of fibrous laminae parallel to the surface. The fibrils appear to connect these laminae by parabolic arcs. Bouligand (1965) proposed that the fibrils are arranged helicoidally. The helicoid model was

subsequently disputed by Dennell (1973) who found that laminae were discrete and separable sheets as opposed to being artifacts as the helicoid model would imply.

The exocuticle usually has smaller laminar spacing than in the outer endocuticle. This portion of the procuticle is secreted at premoult and resists digestion by moulting fluids. The exocuticle and the epicuticle are the components of the exuviae and are most commonly found preserved as fossils.

The endocuticle constitutes the largest portion of the procuticle in most crustaceans but is reabsorbed during premoult. There are two recognizable layers in the endocuticle, 1) the outer calcified principal layer, and 2) the inner uncalcified membranous layer (Drach 1939).

5.2.3 Moulting and growth.

As with other arthropods, crustaceans shed their cuticle and form new cuticle by a process called ecdysis. Pronounced biochemical changes occur during the moult cycle which result in the absorption of the endocuticle and the formation of an ecdysial membrane (Travis 1954, 1955, 1957). The ecdysial membrane is shed along with the exocuticle and the epicuticle (Stevenson 1980). The study of the cuticular changes which occur during the moult cycle may be important in recognizing various moult stages in the fossil crustacean.

The primary method by which crustaceans harden their cuticle is by the deposition of calcium salts. The principal salts responsible are $CaCO_3$ and $Ca_3(PO_4)_2$ which are deposited as calcite and hydroxyapatite (Neville 1975). The distribution of these salts within the cuticle may give an indication of the habits and habitat of the animal (Mills *et al.* 1976). In the crayfish the concentration of calcium in the cuticle decreases with age in *Engaeus fossor*, while in *Geocharax falcata* the concentration remains constant through life. This difference is attributed to the burrowing habits of these crustaceans and the need for protection from the environment. The extent of calcification of the various parts of the crustaceans depends on which parts are considered more important to the crustacean especially in low calcium waters (Mills *et al.*

1976). The calcium salts fill the spaces between the chitin fibrils which would have otherwise been filled with protein.

Growth in arthropods occurs at ecdysis. Under good conditions, it has been suggested that a typical arthropod can double its weight and increase its linear size by 1.26 times. It is more likely, however, that an arthropod will not increase in size at a constant rate at each ecdysis (Aiken 1973, 1980). Size increase of juveniles is greater than that of adults in some crustaceans at least (Mauchline 1977). The different stages of ecdysis can be recognised in the living animal by the rigidity of certain parts of the cuticle. Three stages can be clearly identified on this basis: metecdysis; anecdysis; and proecdysis.

Metecdysis (stages A, B and C) occurs immediately after ecdysis and is characterized by the mineralization of the exocuticle and the secretion of the endocuticle. The pleopods of lobsters during metecdysis appear striated due to rows of large cells.

Anecdysis (late stage C) is characterized by the completion of the membranous layer and the storage of organic reserves in the midgut gland and muscle for an extended period of time. The pleopods have a normal appearance.

Proecdysis (stages D_{0-4} and E) marks the start of a new period before ecdysis which occurs in the active phase of stage E. During stage D , the pleopods show cuticular ripples due to the reabsorption of the endocuticle. The new epicuticle and exocuticle are formed during the period of proecdysis.

Table 5.2 Summary moult cycle of *Homarus* (based on Aiken 1973, Table 1, p94).

Stage	General Characteristics	Duration (%)
A	Integument soft, mouthparts and tips of pereiopods hard; able to eat exuviae.	1.4
B	Integument flexible; secretion of new endocuticle begins.	2.0
C	carapace rigid posterodorsally to rostrum becoming rigid elsewhere towards end of stage	52.6
D_{0-1}	Passive anecdysis becoming proecdysis with the retraction of the epidermis from the cuticle and the formation of new epicuticle.	>35
D_{2-3}	New exocuticle is formed and extensive reabsorption of minerals from the exoskeleton.	16.0
E	*Passive phase*: increased water absorption; ecdysial sutures open but thoraco-abdominal membrane intact. *Active phase*: thoraco-abdominal membrane ruptures; carapace is thrown forward as animal emerges.	

5.3 Crustacean Phylogeny.

5.3.1 The primitive malacostracan crustacean.

Crustacea were thought, until recently, to have evolved from a soft bodied segmented arthropod similar in form to some of those found in the Middle Cambrian Burgess Shale of British Columbia (Briggs 1983). At this early stage in their development, only two extant crustacean subclasses are represented, the Phyllocarida and the Ostracoda, amongst a number of extinct taxa, of which the only recognizable crustacean is the bivalve phyllocarid *Canadaspis*. There are also a number of other bivalved crustaceans which bear some

resemblance to the Branchiura, although probably unrelated (Briggs 1983). As these were the earliest preserved crustacean remains, it was thought that the cephalocarids could have represented the likely ancestor of the malacostracans.

The most primitive crustacean is now thought to have been similar in form to the Carboniferous to Recent group, Remipedia, rather than to the cephalocarids (Cisne 1982, Hessler *et al.* 1982, Schram 1983a, 1986, Briggs 1983). The form of the primitive crustacean limb has been the subject of much discussion and the theories centre around a polyramous and foliaceous form, as in the Cephalocarida, or a biramous paddle, as in the Remipedia. A preliminary study involving all known crustacean groups supports the biramous remipedian limb as being primitive (Schram 1986).

Burkenroad's (1963) suggestion that the Eucarida may have evolved from a primitive eumalacostracan shrimp is now generally accepted (Schram 1986). However, his suggestion that the Decapoda differentiated from the Eucarida in the Permian has since been shown to be false due to the discovery and redescription of Carboniferous decapods (Schram *et al* 1978, Schram and Mapes 1984).

5.3.2 Higher classification of crustacean taxa.

The classification of the Crustacea is intimately related to their phylogeny and should be based on an accepted phylogenetic scheme. Much of the latest discussion on the classification of the Crustacea has centred around the acceptance or rejection of the caridoid facies as a taxonomically valid set of characters (Hessler 1983, Schram 1983b, 1984, 1986). The caridoid facies are not thought to be acceptable, despite the subjectivity involved in the recognition of apomorphies, as there are a number of inherent convergences (Schram 1984).

Another problem arises when dealing with fossil Crustacea as, not only are the soft internal body tissues rarely preserved, but, the hard parts, such as limbs, also have a limited preservation potential (Schram 1982, see Chapter 4). This results in a classification of fossil Crustacea based almost entirely on external

morphologies. Their relationship to extant taxa, which is important to phylogenetic interpretations, is limited to the recognition of similar external morphologies, and any inferred soft tissue distribution. This decreases the confidence with which fossil taxa may be placed with extant taxa, although, taxonomic affiliations may be proposed where there are overwhelming morphological similarities (McLaughlin 1980).

The problem of identifying which characters are important to the various taxonomic levels and which characters are environmentally induced can be solved by identifying a number of characters which are common to a number of taxa and assessing the degree of conservatism they exhibit between taxa. Crustaceans are mostly similar in basic body plan with the exception of the Cirrepedia and various parasitic groups. Amongst free living taxa it is possible to differentiate between different taxa on the basis of the nature of the carapace, the number of body somites, and the tagmata of the body (McLaughlin *et al.* 1982). At progressively subordinate levels, armature and ornamentation may become more important in differentiating taxa. In practice, many carcinologists rely on gross morphological structures as well as on the mouth parts, sexual specialization, and colour patterns as diagnostic characters. It is also important to note that there may be a significant amount of intraspecific variation, which should be recorded in the diagnosis of any taxa.

Conservative diagnostic characters are important to any diagnosis, so as to determine the interrelationship between taxa (McLaughlin *et al.* 1982). These characters may be highly subjective and must be regarded sceptically. More objective methods of taxonomic differentiation are available, such as the application of the numerical taxonomy, although this is thought to have limited application to crustacean studies (McLaughlin *et al.* 1982).

The most recent classification of Crustacea offered by Schram (1986), uses cladistic analysis to produce the most parsimonious classification based on apomorphic characters. Many of the apomorphic characters used by Schram are, however, impossible to resolve in most fossil material due to their poor

preservation potential. This reduces the number of characters which can be used in the classification of the fossil material from the Carboniferous.

The classification, below, proposed by Schram (1986), is thought to be broadly acceptable to the level of infraorder (‡ = fossil taxa only).

Phylum Crustacea Pennant, 1777

Class Malacostraca Latreille, 1806

Subclass Hoplocarida Calman, 1904

Order Aeschronectida ‡ Schram, 1969

Order Palaeostomatopoda ‡ Brooks, 1962

Order Stomatopoda Latreille, 1817

Suborder Archaeostomatopodea ‡ Schram, 1969

Suborder Unipeltata Latreille, 1825

Subclass Eumalacostraca Grobben, 1892

Order Syncarida Packard, 1885

Suborder Bathynellacea Chappuis, 1915

Suborder Anaspidacea Calman, 1904

Suborder Palaeocaridacea ‡ Brooks, 1962

Order Belotelsonidea ‡ Schram, 1981

Order Euphausiacea Dana, 1852

Order Amphionidacea Williamson, 1973

Order Decapoda Latreille, 1803

Suborder Dendrobranchiata Bate, 1888

Suborder Eukyphida Boas, 1880

Infraorder Procaridídea Felgenhauer and Abele, 1983

Infraorder Caridea Dana, 1852

Suborder Euzygida Burkenroad, 1981

Infraorder Stenopodidea Huxley, 1879

Infraorder Uncinidea ‡ Beurlen, 1930

Suborder Reptantia Boas, 1880

Order Eocarida Brooks, 1962

Order Mysida Boas, 1883

Order Lophogastrida Boas, 1883

Order Pygocephalomorpha ‡ Beurlen, 1930

Order Mictacea Bowman *et al.*, 1985

Order Edriophthalma Leach, 1815

Suborder Isopoda Latreille, 1817

Suborder Amphipoda Latreille, 1816

Order Thermosbaenacea Monod, 1927

Order Hemicaridea Schram, 1981

Suborder Cumacea Kröyer, 1846

Suborder Tanaidacea Dana, 1853

Infraorder Anthracocaridomorpha ‡ Sieg, 1980

Infraorder Apseudomorpha Sieg, 1980

Infraorder Neotanoidomorpha Sieg, 1980

Infraorder Tanaidomorpha Sieg, 1980

Suborder Spelaeogriphacea Gordon, 1957

Class Maxillipoda Dahl, 1956

Subclass Tantulocarida Boxshall and Lincoln, 1983

Order Tantulocaridida Boxhall and Lincoln, 1983

Subclass Branchiura Thorell, 1864

Order Arguloida Rafinesque, 1815

?Order Pentastomida Rudolphi, 1819

Subclass Mystacocarida Pennak and Zinn, 1943

Order Mystacocaridida Pennak and Zinn, 1943

Subclass Ostracoda Latreille, 1806

Order Bradoriida ‡ Mathew, 1902

Order Phosphatocopida ‡ Müller, 1964

Order Leperditicopida ‡ Scott, 1961

Order Palaeocopida Henningsmoen, 1953

Order Myodocopida Sars, 1866

Order Podocopida Sars, 1866

Subclass Copepoda Milne-Edwards, 1840

Order Calanoida Sars, 1903

Order Misophrioida Gurney, 1933

Order Harpacticoida Sars, 1903

Order Mormonilloida Boxhall, 1979

Order Siphonostomatoida Thorell, 1859

Order Monstrilloida Sars, 1903

Order Cyclopoida Burmeister, 1834

Order Poecilostomatoida Thorell, 1859

Subclass Thecostraca Gruvel, 1905

Order Facetotecta Grygier, 1984

Order Rhizocephala Müller, 1862

Order Ascothoracida Lacaze-Duthiers, 1880

Order Cirripedia Burmeister, 1834

Infraorder Acrothoracica Gruvel, 1905

Infraorder Thoracica Darwin, 1854

To further analyse the above classification with respect to the fossil genera from the Carboniferous, it is necessary to recognise which gross morphological characters are preserved in the fossils, and which groups of these characters can be used to distinguish between ordinal level groupings.

5.3.3 Development of malacostracan caridoid and hoploid morphologies.

Two basic morphologies have been recognised in malacostracans; the caridoid facies of Calman (1909) and the hoploid facies of Schram (1983a). The characteristics of the caridoid facies include;

1) a carapace enveloping the thoracic region,

2) movable stalked eyes,

3) biramous first antenna,

4) natatory exopods on the thoracic limbs,

5) an elongate, ventrally flexible abdomen,

6) a tail fan of lamellar uropods on either side of a telson,

to which Hessler (1983) added;

7) complex and massive abdominal musculature serving strong ventral flexion,

8) internal organs mainly excluded from the abdomen,

9) pleopods I-V similar, biramous, and natatory,

The hoploid facies presented by Schram (1983a) includes;

1) triramous antennules,

2) an antennal scale of two joints,

3) thoracopods with three segment protopod, and four segment endopod,

4) an abdomen with distinct ("quasi-caridoid") musculature,

5) pleopod gills dendrobranchiate,

6) possible fusion of the anterior somite to achieve a six-segment from a seven segment abdomen.

The occurrence of the external caridoid features in the earliest eumalacostracan fossils supports the concept of a caridoid facies as being the archaetypical state. The Anaspidacea are included as caridoid despite the lack of a carapace, as they have most of the necessary characters including the escape reaction (Hessler 1983).

The reason why, and how, the crustaceans developed caridoid features plays an important part in the study of crustacean phylogeny. Towards the end of the Devonian, the first crustaceans exhibiting a full complement of caridoid features emerged, and as early as the Lower Carboniferous there were many of non-caridoid morphologies which developed, such as the tanaids (Hessler 1983). Due to the preservation potential of the crustaceans (see Chapter 4), much of the important details of the early evolution of the Eumalacostraca and Hoplocarida may not be preserved (Hessler 1983). The most obvious advantage of the development of the caridoid abdomen is the caridoid escape reaction which involves the rapid ventral flexion of the abdomen to produce vertical lift and backwards motion. Another advantage of the caridoid features is in the increased maneuverability provided by the tail fan and the antennal scale. The primitive eumalacostracans may have used the tail fan for steering while swimming, a function for which it is sometimes used in extant Hoplocarida and Eumalacostraca (Hessler 1983). The apparent rapid explosion of crustaceans with caridoid and hoploid features testifies to the success of the development of these characteristics. The wide variety of forms with variably developed caridoid and hoploid features within the same basic body plan, resulting probably from a response to functional specialization, is probably another reason for the success of the Malacostraca (Hessler 1983). The reason for the development of the caridoid escape reaction may have been, in part, due to a response to the development of the crossopterygians (Dahl 1983).

The loss of the seventh abdominal somite is thought to be due to the fusion of

the seventh abdominal somite with that of the sixth. This would have facilitated the development of the tail fan by bringing the pleopods of the sixth abdominal somite closer to the telson to form the uropods of the tail fan (Hessler 1983). In the embryonic stages of *Hemimysis*, a seventh abdominal somite which fuses in the adult stages has been recorded (Manton 1928). In the Lophogastridae a groove across the sixth abdominal somite is also thought to represent the remnants of the seventh somite (Manton 1928).

Hoplocarids pose another central problem in the phylogenetic interpretation of the Malacostraca as they possess many of the caridoid features, but do not have a fully caridoid abdominal musculature. The relative importance placed on this by various authors resulted in the Hoplocarida being either classified within the Eumalacostraca (*sensu* Schram 1986), or as a separate subclass. The arguments for retaining them within the Eumalacostraca are that the Hoplocarida represent an evolving caridoid condition, and the fusion of the abdominal somites to form six segments occurred posteriorly rather than anteriorly (Hessler 1983). The arguments against this are based on the acceptance of a different set of characters, the hoploid facies, and that the fusion of the abdominal somites to leave six segments occurred in the anterior portion of the abdomen (Schram 1969, 1973, 1983a, Hessler 1983, Kunze 1983).

The caridoid facies has limited use in classification as similarities of form are meaningless without a firm understanding of the functional development of the animal in question. The recognition of these facies is highly subjective, and a more objective cladistic method has been used to help resolve the phylogenetic distance between the Hoplocarida and other malacostracan taxa (Schram 1986). The technique of assigning plesiomorphy and apomorphy to various characters, however, is also highly subjective, and only synapomorphous characters should be used in phylogenetic analysis (Schram 1986). The recognition of convergence is, therefore, dependent on the initial definition of apomorphy. The uncertainty of phylogenetic analysis may be reduced by the application of *Baupläne*, or morphotypes, with an understanding of their function (Schram 1983a). The application of a cladistic approach demands that the accepted hypothesis contains the least number of convergences (Schram

1984). If the carapace is taken to be a derived character (Dahl 1983), for example, more convergences have to be accepted than if the carapace is taken to be primitive (Schram 1984). The acceptance of the caridoid facies (*sensu* Hessler 1983) also introduces a greater number of convergences, which suggests that it is more plausible to accept the separation of the Hoplocarida from the Eumalacostraca (Schram 1984). However, Schram (1986; p541) indicated that Hessler (1983) did, in fact, produce a similar phylogeny despite the different approach, although the taxonomic hierarchy was different.

5.4 The classification of Carboniferous crustaceans from Great Britain.

Most of the Carboniferous crustacean genera are easily distinguishable on the basis of gross morphological differences, such as the shape of the carapace, the abdomen, and the tail fan, and the presence or absence of various features, such as the carapace. The relative lengths of the abdominal tergites, the shapes of the pleura, the shapes of the telson and the uropods, the sculpturing of the carapace, the relative length of the rostrum, and the form of the limbs also help to further differentiate between groupings.

The relationship between fossil genera and ordinal level classifications is sometimes problematic, when only a few characters are used, as convergences of apomorphic characters could result in false relationships being constructed. The problem of applying characters used in the classification of extant taxa is that many of these characters are not preserved in the fossil specimens, and therefore only inferred to exist. It is, therefore, necessary to construct a classification, which can be used with a certain amount of confidence, for fossil genera. The characters used in this classification can then be compared generally to their presence in extant taxa. To accept any classification formulated in this way, it is important to consider groups of synapomorphic characters as non-convergent, despite the possibility of convergence of individual characters. In other words, the more characters a particular crustacean has in common with another, the more likely it is that they are closely related, and the less likely it is due to convergence. On the basis of this

assertion, it is possible to recognise several crustacean groups in the Carboniferous which may represent antecedents to extant taxa.

The classification presented here is based on previously published diagnoses and descriptions, as well as new data, of eighteen British Carboniferous genera. The new data comes from the study of the crustacean genera, *Tealliocaris*, *Palaemysis*, *Crangopsis*, *Tyrannophontes*, *Minicaris*, and *Cyclus*, which are described more fully in later sections of this chapter. Whether a character is apomorphic or plesiomorphic, is not thought to be important in an analysis of the classification of the fossil Crustacea. The important feature of this classification, is that groups of characters are as close to being conservative, within each crown grouping, as possible. For this reason, the extant Orders Syncarida, Decapoda, Euphausiacea, Mysida, Stomatopoda, and Tanaidacea, include all possible morphologies represented within the context of the preservable characters used for the classification of the fossil genera. The data was analysed using the computer program MacClade (version 2.1, written by Wayne Maddison, W. P. and D. R. Maddison, 1987, Harvard University).

5.4.1 The classification of the malacostracan taxa.

The difficulty in recognizing morphological convergence in the Malacostraca is partly a function of a particular authors ability to recognise particular features. Evidence for features such as thoracic brood pouches, or maxillipeds, are mostly equivocal and have to be treated carefully. The Order Pygocephalomorpha, for example, is diagnosed as having a brood pouch and described as having two maxillipeds, and, therefore, cannot be classified with the Decapoda. On a purely gross morphological basis, however, it appears that the pygocephalomorphs have much in common with the decapods and may represent ancestral forms of the latter. *Tealliocaris* is particularly interesting as it has a suite of characters which place it even closer to the decapods. This assumes that the "oöstegites" described by Brooks (1969), and Schram (1979), are in fact epipods, as was suggested by Briggs and Clarkson (1985a). The number of "walking" limbs in *Tealliocaris* is also interpretative, as only five limbs ever seem to extend beyond the lateral margins of the carapace (Schram 1979, fig. 33). The anterior three thoracic limbs could be maxillipeds, although,

the second and third limbs do not appear to be morphologicaly different from the posterior five, but are shorter and anteriorly directed. Although their function cannot be determined in the fossil, these limbs can be speculatively compared with maxillipeds of some extant decapods.

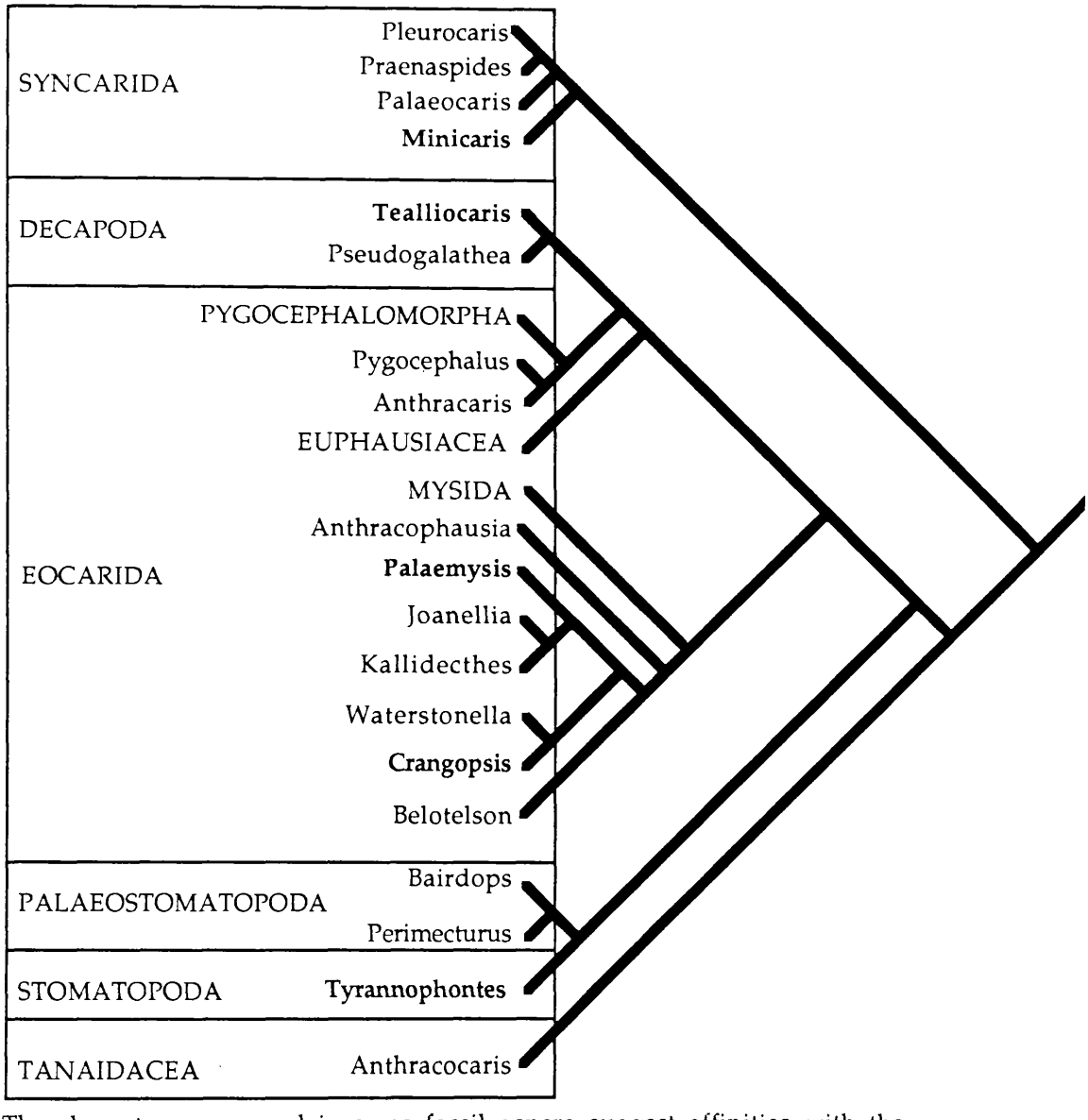
The classification of the Carboniferous crustacean genera presented here is based on the following characters;

1. tail-fan morphology: deltoid, rectangular, or subrectangular; open (without uropodal membranes).
2. telson morphology: triangular or subrectangular; complex (with furcal lobes).
3. 6th abdominal somite: longest somite; not longest somite.
4. 3rd abdominal somite: enlarged; not enlarged.
5. pleura of 2nd abdominal somite: rounded (overlap of 1st and 3rd); undifferentiated.
6. 1st abdominal somite: shortest; not shortest.
7. pleopods: plates; flagellar.
8. carapace: present; absent.
9. shape of cervical groove: ∏; V; absent.
10. rostrum: present; absent or reduced.
11. anterior thoracopods: maxillipeds; no maxillipeds.
12. subchelate thoracopods: none; some.
13. thoracopod morphology: "walking" stenopods; flagellar.
14. epipods: large; absent or greatly reduced.
15. carapace: covers thorax; thoracic tergites visible.
16. antennules: 3 flagella; 2 flagella.
17. antennae: 2 flagella; single flagella.
18. thoracopods chelate: none; some.
19. seminal receptacle: present; absent.
20. number of "walking" limbs: <5; 5; 6; 7; 8.

The resulting most parsimonious clade which is produced from an analysis of the above mentioned morphological characters, identifies five major crown

groups which broadly correspond to extant orders of the Malacostraca. The different recognised morphologies within these orders were compared with the data from the fossil genera and were found to group in the following manner;

Figure 5.2 Cladogram showing the possible relationships between Scottish fossil genera (those represented in the Manse Burn Formation in bold).



The characters preserved in some fossil genera suggest affinities with the Decapoda, the Euphausiacea, the Pygocephalomorpha and the Mysida. These genera are, therefore, classified together in a single crown group, the Eocarida.

Tealliocaris, however, is thought to represent a close ancestor to the Decapoda, as it does not show any morphological differences to the total group

morphologies of this order. The Pygocephalomorpha and the Euphausiacea may also be distantly related to each other, and also to the Decapoda. The Mysida are not far removed from the basic morphological plan of the Eocarida crown group, although, where the genera are distinctly mysid, they have been placed within this separate order.

The lamellae of *Tealliocaris* were described by Briggs and Clarkson (1985a, p186) as being in the position of a pereiopodal epipod which would not be homologous with oöstegites as previously indicated by Schram (1979). The presence of oöstegites were also used as evidence for affinities with the Order Podophthalmia by Peach (1908, p20), the Mysidacea by Schram (1979), and the Order Pygocephalomorpha by Brooks (1962). Epipods are common amongst a number of crustacean taxa including the Decapoda. The lamellae may be homologous to the pereiopodal epipods of many other extant crustacea such as the syncarid *Anaspides tasmaniae* or the eukyphid *Procaris ascensionis* (Schram 1986, p76, p256).

The laterally expanding pleura of the second abdominal somite, in *Tealliocaris*, is a common feature of eukyphidan decapods such as *Stylodactylus amarynthis* (Schram 1986, p261). The large third abdominal tergite extending to partially overlap the fourth is also common amongst the Eukyphida and can be seen in *S. amarynthis* and also *Procaris ascensionis*. The terminal lobe or membrane of the telson on *Tealliocaris*, is similar to that of *Astacus nobilis* (Huxley, 1880, p233), although the median and lateral ridges of the telson of *Tealliocaris* extend over the membrane.

The modern decapod, *Procaris*, has the most characters in common with *Tealliocaris*. It is surprisingly similar in terms of limb morphology and body plan, although the sculpturing of the integument is more intense in *Tealliocaris*. *Procaris* was first discovered in 1972 in Hawaii (Holthuis 1973) and Ascension Island (Chace and Manning 1972) and has since stimulated much interest amongst carcinologists. More recent discoveries of species belonging to this superfamily have been made in Bermuda (Hart and Manning 1986) and Hawaii (Kensley and Williams 1986). Chace and Manning (1972, p14)

suggested that *Procaris* is the most primitive of living decapods and produced a diagnosis for *Procaris* (Chace and Manning 1972, p13) which could easily apply for the generic description of *Tealliocaris*. There are many characters common to both *Tealliocaris* and *Procaris*, such as the achelate pereiopods, long annular pereiopodal exopods, large epipods, and the shape of the pleura of the second abdominal somite.

The number of similarities between the *Tealliocaris* and *Procaris*, suggests that convergence is unlikely. Although it is possible that some of the gross morphological similarities between these genera could be as a result of convergence, it must be considered more likely that the overwhelming similarities are due to them belonging to the same crustacean group.

Another crustacean which has many similarities with extant taxa is *Tyrannophontes*. *Tyrannophontes*, is thought to be a stomatopod rather than a palaeostomatopod due to the specialization of the thoracopods into subchelate anterior limbs and blade-like posterior limbs, and the carapace which extends dorsally only as far as the sixth thoracic tergite. In the palaeostomatopods this is thought not to be the case (Schram 1969).

5.4.2 The systematic position of *Cyclus*.

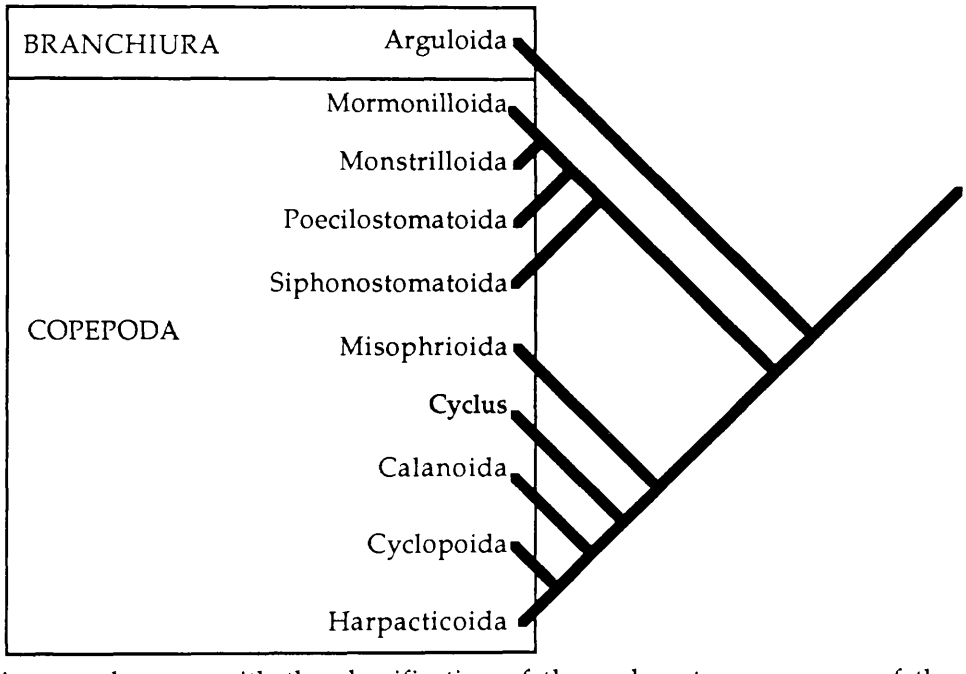
As has already been discussed in section 5.1.6, there have been many suggestions as to the affinities of *Cyclus*. The most likely, and most generally accepted position of *Cyclus*, is either with the Copepoda or with the Branchiura, which are both subclasses of the Class Maxillipoda (Glaessner 1969). In this section a number of morphological characters have been chosen in an attempt to determine the most likely systematic position of *Cyclus* based on new evidence obtained from a study of the specimens collected from the Manse Burn Formation. These characters include:

1. Antenna: two flagella; one flagella;
2. Head shield with carapace: present; absent;
3. Subchelate limbs: 0; 1; 2;
4. 'walking' limbs: 4; 5; 0;

5. Abdominal somites: 5; unsegmented;
6. Tail fan: caudal furca; cleft abdomen;
7. Antennules: short; long;
8. Antennules: 10 or less articles; greater than ten articles;
9. Sixth thoracopod in male: modified sex organ, not sex organ or short/absent;
10. Body form: elongate; ovate; highly modified;
11. Adaptation: mostly free living; modified parasitic;
12. Maxillules: developed as suckers; not suckers;
13. Body flexure between the 6th thoracic somite and the first abdominal: yes; no;

It was found that *Cyclus* could be easily classified with the less modified copepods, such as the Calanoida and the Misophrioida.

Figure 5.3 Cladogram showing the possible relationships between extant copepods and branchiurans in relation to *Cyclus* (in bold).



As was the case with the classification of the malacostracans, some of the characters used in this classification are ubiquitous within the Copepoda, and some common to both the Copepoda and the Branchiura, such as the single flagella of the antennae. As the Misophrioida still have a carapace fold on the maxillipedal segment, it is likely that *Cyclus* is more closely related to

this order than the other copepod orders. The systematic position of *Cyclus* is with the Copepoda and, although affinities with the Orders Misophrioida and Calanoida can be shown, there is not sufficient evidence to assign *Cyclus* to any extant order. Gall and Grauvogel (1967) suggested the use of a separate Subclass Halicyna to include the Families Cyclidae, Hemitrochiscidae, Mesoprosoponidae and Halicynae. As *Cyclus* can, at least, be shown to be a copepod, the subclass proposed by Gall and Grauvogel should be considered at the ordinal level (Order Halicyna).

5.5 Systematic descriptions of the crustaceans of the Manse Burn Formation.

Class Malacostraca Latreille, 1806
Subclass Hoplocarida Calman, 1904
Order Stomatopoda Latreille, 1817
Genus *Tyrannophontes* Schram, 1969

Type species.- *Tyrannophontes theridion* Schram, 1969. From the Bear Gulch Member, Montana (Namurian).

Emended diagnosis (after Schram 1969 and Factor and Feldmann 1985).- Fossil stomatopod with the rectangular carapace extending mid-dorsally to about the fourth thoracic somite. The sixth thoracic somite is at least partially, laterally exposed. Uropodal exopod and endopod blade-like without diaeresis. Telson base rectangular and elongate with terminal spike developed posteriorly.

Tyrannophontes pattoni (Peach, 1908),
Plate 5.1a-c; Figs. 5.4 a-c, 5.5.

1885 *Palaesquilla pattoni* [nomen nudum] Peach. Patton and Coutts, p327.

1888 *Palaesquilla pattoni* [nomen nudum] Peach. Coutts, p173.

1908. *Perimecturus pattoni* (Peach). Peach, p51-53, pl. 6, fig. 9.

1979. *'Perimecturus' pattoni* Peach. Schram, p60-61, fig. 22.

Lectotype (after Schram 1979, p60, fig. 22).- RMS 1887.25.1059 from the Manse Burn Formation of East Kilbride (Plate 5.1a, Fig. 5.4 c).

Diagnosis.- Posterior thoracic limbs blade-like. Margins of abdominal pleura smooth and broadly rounded. Margins of tailfan undecorated with spines or setae. Telson spike at least half the length of the entire triangular telson.

Material.- Only three specimens of this genus are known from the Manse Burn Formation. RMS 1887.25.1059 from East Kilbride, Lanarkshire, one from Bearsden (Plate 5.1c), and one from the Red Cleugh Burn (Plate 5.1b).

Description.- Of the three specimens from the Manse Burn Formation, none have the anterior portion very well preserved. The carapace is poorly preserved in two specimens and only the posterior margin in the other. No rostrum can be seen in any of the specimens and the carapace appears to lack any ornamentation. The cuticle is thin (≈40μm), with patchy preservation, perhaps due to a high organic content which is common in extant hoplocarid crustaceans (Kelly 1901).

Two of the posterior thoracic limbs are preserved in one specimen (see Plate 5.1a; Fig. 5.4c). These are modified bladed limbs which may have been used for swimming. The anterior limbs are less well preserved, but the proximal articles of some appear to be posteriorly directed and the more distal articles point anteriorly. At least three of the thoracic tergites are not covered by the carapace postero-dorsally.

All six of the abdominal somites are subequal in length and are approximately 1.5 times the length of the posterior three thoracic somites. The pleura of the abdominal somites are posteriorly rounded. The pleopods are not preserved.

The telson terminates posteriorly in a median spike. The median spike is at least half as long as the triangular telson base. The uropodal exopod and endopod are lobate and extend almost the full length of the telson. The uropods

Plate 5.1

a) Lectotype of *Tyrannophontes pattoni* from the Shrimp Member at East Kilbride (RMS 1887.25.1059; X6.5). Arrow pointing to rear-most thoracic limbs.

b) Specimen of *Tyrannophontes pattoni* from the Red Cleugh Burn locality (HM A21500a; X3.5).

c) Specimen of *Tyrannophontes pattoni* from the Manse Burn locality (HM; X6.25).

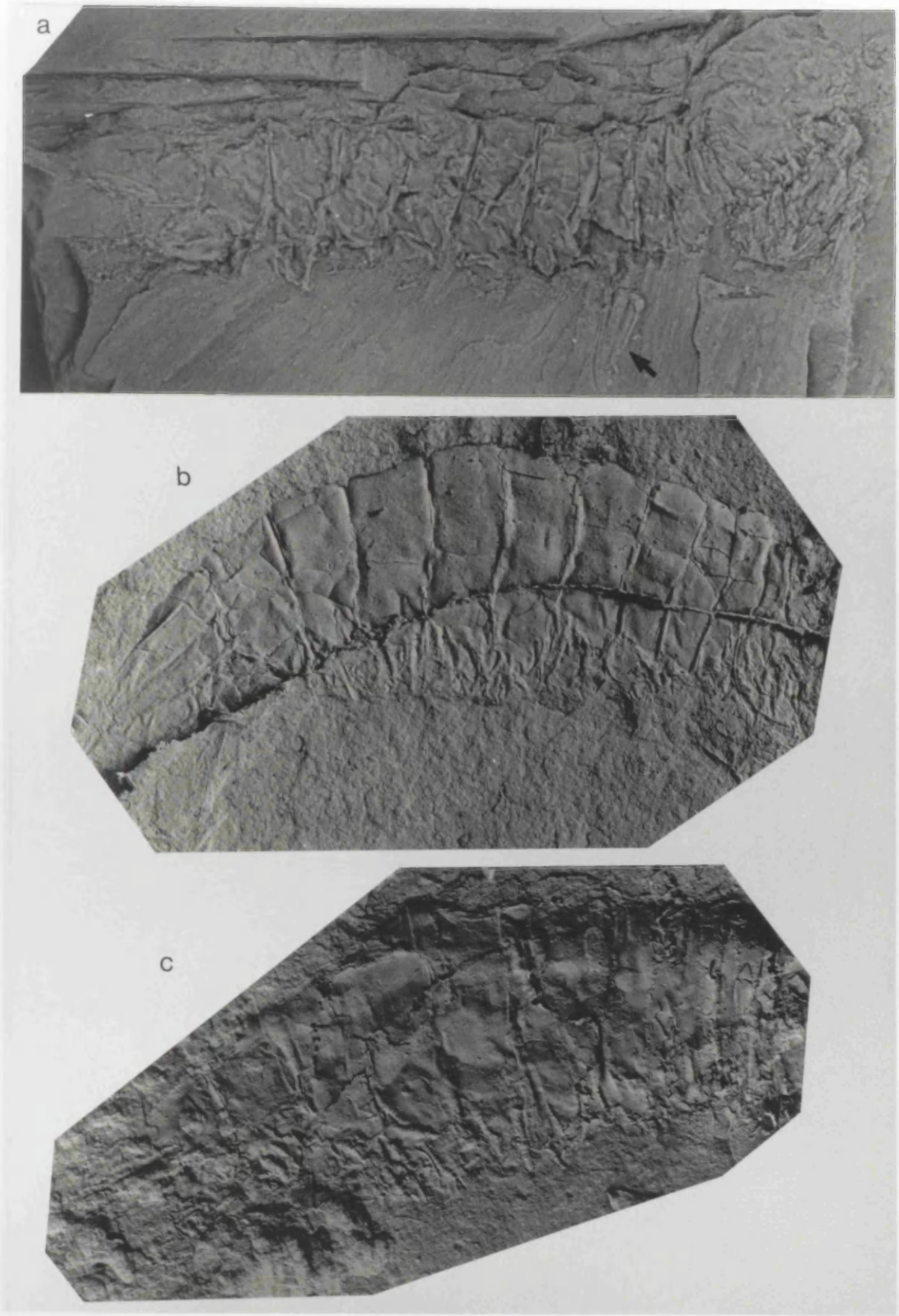

a
b
c

Figure 5.4

a) Specimen of *Tyrannophontes pattoni* from the Red Cleugh Burn locality (HM A21500a; scale-bar = 1cm).

b) Specimen of *Tyrannophontes pattoni* from the Manse Burn locality (HM; scale-bar = 0.5cm).

c) Lectotype of *Tyrannophontes pattoni* (RMS 1887.25.1059; scale-bar = 0.5cm).

(c=carapace; t8=eighth thoracic tergite; a1=first abdominal somite; a6=sixth abdominal somite; te=telson; tes=telson spine; th=thoracic appendages; u=uropods).

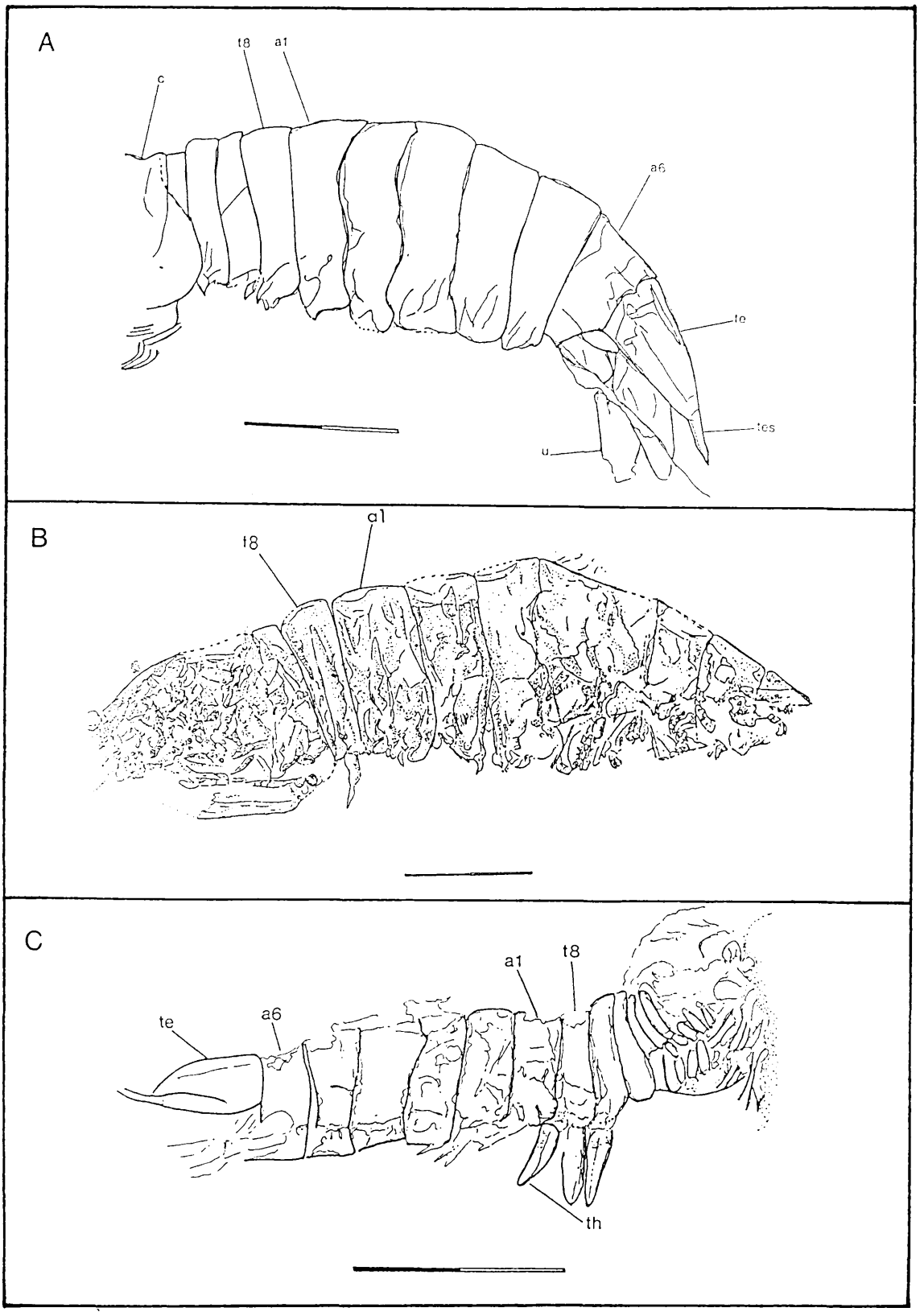
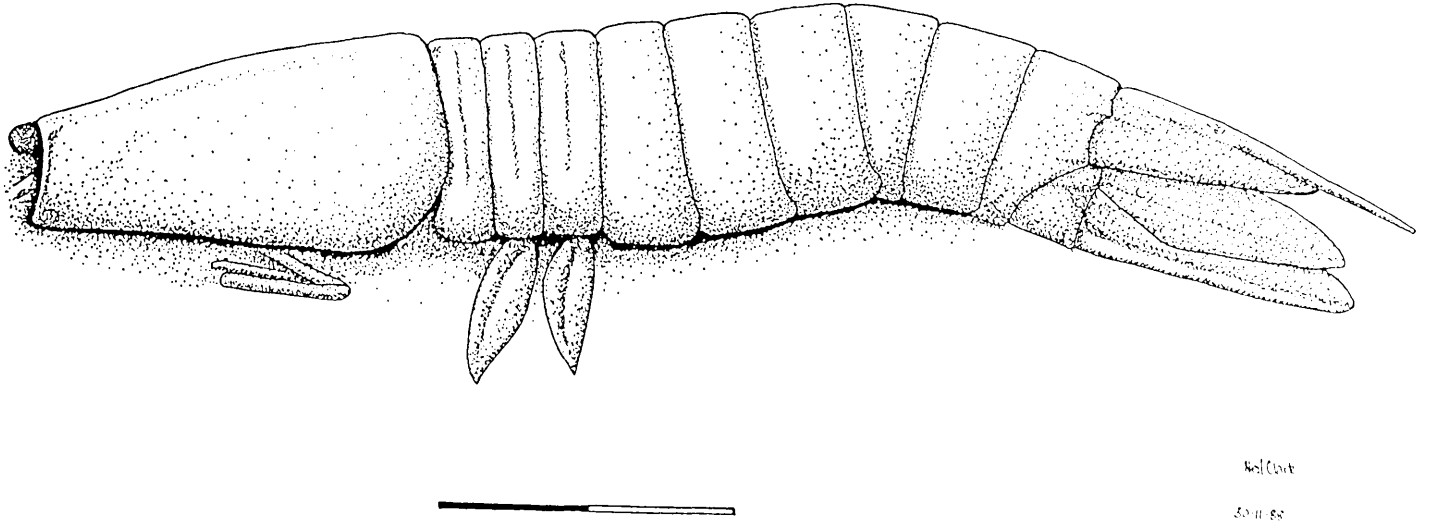

A
t8
a1
c
a6
te
tes
u
B
t8
a1
C
te
a6
a1
t8
th

Figure 5.5

Reconstruction of *Tyrannophontes pattoni* (scale-bar ≈1cm).



lack diaeresis and are unornamented.

Remarks.- *Tyrannophontes* is the least common member of the crustacean assemblage from the Manse Burn Formation, and has been found from the upper part of the Shrimp Member and the base of the Posidonia Member. Palaeostomatopods also occur elsewhere as minor elements associated with high diversity crustacean assemblages at Granton (Briggs *et al. in prep.*), at Glencartholm (Schram 1979, 1983c), and at Bear Gulch (Schram 1969, 1982, Factor and Feldmann 1985). As these crustaceans are minor components of their respective assemblages, and due to the adaptation of the thoracic limbs as subchelae, it is likely that they represent a predatorial crustacean.

The blade-like uropodal exopods and endopods, the three exposed thoracic somites, and the differentiation of the blade-like posterior thoracic limbs from the anterior thoracic limbs are the characters which are used here to differentiate *Tyrannophontes* from *Bairdops* and *Perimecturus*. Schram (1979) did not have the necessary features of the tail fan preserved to place it with the tyrannophontids, although he noted that the blade-like posterior thoracopods were similar in character to those seen on tyrannophontids. The two new specimens allow a more positive comparison to be made between the genus *Tyrannophontes* and the specimens from the Manse Burn Formation.

The species represented in the Manse Burn Formation differs from *Tyrannophontes theridion* in that it does not have the spines on the lateral margin of the uropodal exopod, the median spine of the telson lacks lateral spines, and the posterior thoracic limbs are more blade-like.

Subclass Eumalacostraca

Order Decapoda

Genus *Tealliocaris* Peach 1908, p9.

Type species.-*Anthrapalaemon? woodwardi* Etheridge 1877, p863, pl.27, *Tealliocaris woodwardi* (Etheridge 1877). Peach 1908, p18-22, pl.2, figs. 1-6.

Tournaisian, Lower Carboniferous, from Belhaven Bay, near Dunbar.

Diagnosis. Anterolateral spines on carapace, V-shaped cervical groove, paired postorbital spines, achelate thoracopods, large third abdominal tergite extending to cover most of the fourth, tergite of the second abdominal somite expands laterally.

Tealliocaris woodwardi (Etheridge 1877),
Plate 5.4c, 5.5a, b, d; Figs. 5.5b, c, 5.8a, 5.11a.

1877 *Anthrapalaemon? woodwardi* Etheridge. p863, pl.27.

1879 *Anthrapalaemon woodwardi* Etheridge 1877. Etheridge. p468, pl. 23, figs.4-9.

1908 *Tealliocaris woodwardi* (Etheridge 1877). Peach. p18, pl.2, figs. 1-6.

1908 *Tealliocaris loudonensis* Peach. p9, pl.1, figs 1-7.

1908 *Tealliocaris tarrasiana* Peach. p26, pl.3, figs. 13-16.

1979 *Tealliocaris woodwardi* (Etheridge 1877) Schram. p75, figs. 32-33.

1982 *Tealliocaris loudonensis* Peach 1908, Dewey and Fåhræus. p668, fig. 3, pl.1, figs. 1-4.

1985 *Tealliocaris woodwardi* (Etheridge 1877), Briggs and Clarkson. p175, figs. 1b-e, 2-22, 24.

Material.- Specimens studied were found in a laminated dolostone at Cheese Bay, East Lothian (Hesselbo and Trewin 1984, Briggs and Clarkson 1985) and at Granton, near Edinburgh (Cater 1987).

Emended diagnosis.- One to four spines on outer lateral margin of antennal scale, two transverse grooves on the third abdominal tergite only, one prominent anterolateral spine on carapace, median keel and lateral keels on carapace non-crenulate.

Description.- *T. woodwardi* has already been described in detail by Briggs and

Clarkson (1985a). Since then, several new structures have been found on further specimens. Only these new structures and a reinterpretation of previously described features will be treated here.

The carapace is ornamented with paired post-orbital spines anterior to the V-shaped cervical groove. A maximum of five pereiopods project beyond the lateral margins of the carapace. The V-shaped cervical groove is clearly marked and is associated with other carapace grooves. There is a groove which contours the base of the rostrum connecting with the cervical groove close to the median ridge. This groove also seems to continue laterally beyond the post orbital spines to connect with the cervical groove latero-ventrally. The cervical groove does not connect postero-dorsally, but appears to split into two shallow grooves which almost parallel the carapace ridges. There are five thoracic sternites posterior to the cervical groove.

The arthrodial membrane, which connects the abdomen to the carapace, has three marked ridges which may represent the impression of structures from within the abdominal cavity. The second abdominal somite expands laterally and may partially overlap the lateral edges of the first and third abdominal somites. The third abdominal tergite is extended posteriorly to cover most of the fourth abdominal tergite. Oval processes can be seen on the postero-lateral margin of the second abdominal tergite and the anterolateral margin of the posterior third of the third abdominal tergite. The third abdominal tergite has two transverse grooves one of which terminates at the median ridge (Plate 5·5a).

The telson is made up of two parts. The first is the subrectangular section with a median and two lateral keels. The lateral edges of this section terminate in a spine and sulcus which curves into the two lateral keels. The lateral keels also terminate posteriorly in a spine and narrow sulcus. The second part of the telson, a thin membrane, which has previously been described as a small subcircular flap (Briggs and Clarkson 1985a, p195), is actually much larger than previously thought. The membrane extends from the two lateral spines of the anterior half of the telson to beyond the posterior margin of the lateral ridges. The membrane would give the appearance of a small subcircular flap on

compaction due to the lateral spines of the posterior half of the telson. There is a median spine extending to the extreme distal edge of the membrane which may be ventral to the membrane.

Remarks.- The environment in which *T. woodwardi* occurs does not seem to vary much between localities. Associated faunal elements are rare at Cheese Bay, consisting of ostracodes, fishes, hydroids, scorpionid fragments, and plant fragments (Briggs and Clarkson 1985a, p200). A study of the sediments indicates a thermally stratified lake or brackish lagoon (Hesselbo and Trewin 1984) as being the habitat of *T. woodwardi* at Cheese Bay. At Granton the fauna of bed 'o' of Cater (1987, p30), includes rare ostracodes, gastropods, hydroids, and plant fragments associated with *T. woodwardi* in what has been interpreted as a low-energy stagnant lagoon.

It has previously been postulated that the membrane of the telson was in three parts, two lateral rami and a terminal flap (Schram 1979). The evidence for this was disputed by Briggs and Clarkson (1985a, p195) and a small subcircular single flap was postulated. It is shown here to be a single large membrane. The membranous flap was probably distorted by compaction in most specimens resulting in the small subcircular appearance (see Plate 5.5d).

Although this species does not occur in the Manse Burn Formation, it was necessary to redescribe this species as a comparison. Other species, formally described by Peach (1908) as *Tealliocaris*, were studied in the light of these newly observed structures, to formulate a more complete understanding of this genus. As a result, the species described next were recognised.

Tealliocaris etheridgii (Peach 1881),

Plate 5.2b, 5.4b, 5.5c; Figs. 5.7a, 5.8c, 5.11c.

1882 *Anthrapalaemon etheridgii* Peach. p176, pl.8, figs. 3-3g.

1882 *Anthrapalaemon formosus* Peach. p83, pl.8, fig. 8.

1883 *Anthrapalaemon formosus* Peach 1882. Peach. p512, pl.28, figs. 3-3b.

1883 *Anthrapalaemon etheridgii* var. *latus* Peach. p513, pl.28, figs. 4-4b.

1908 *Tealliocaris etheridgei* (Peach 1881). Peach. p22, pl.3, figs. 1, 2.

1908 *Tealliocaris etheridgei* var. *lata* (Peach 1881). Peach. p23, pl.3, figs. 3, 4.

1908 *Tealliocaris formosa* (Peach 1881). Peach. p27, pl.3, figs. 17, 18.

1979 *Pseudotealliocaris etheridgei* (Peach 1881) Schram. p95, figs. 44, 45.

Lectotype.- BGS 5918 (Schram 1979, fig. 44a) (Plate 5.5b)

Diagnosis.- Nine or more spines on the outer lateral margin of antennal scale, crenulate anterolateral margin of the carapace, median keel of carapace not crenulate, transverse grooves on all except the sixth abdominal tergites, single transverse groove on the third abdominal tergite.

Material.- Specimens of this species come from a thinly laminated grey dolomitic shale with a rich marine fauna at Glencartholm, near Langholm (Middle Border Group, Viséan) (Schram 1979, 1981a, 1983c), and from an impure laminated dolostone at Muirhouse, Granton near Edinburgh (Viséan) (Cater 1987).

Description.- The carapace has paired postorbital spines anterior to the V-shaped cervical groove. The anterolateral margin of the carapace is armed with short spines numbering at least six. The carapace grooves are similar to those seen on *Tealliocaris woodwardi*.

The arthrodial membrane has three marked ridges in a similar manner to that found on *T. woodwardi*. The pleura of the second abdominal somite can be seen to partially overlap those of the first and third, as was first noted by Peach (1882) on *A. etheridgii*. The third abdominal tergite extends to cover most of the fourth. An oval process can be seen on the section posterior to the second

transverse groove of the third abdominal tergite.

The subrectangular telson is armed with two lateral spines, a median ridge and six spines on the postero-lateral ridges.

Remarks.- The fauna associated with *T. etheridgii* at Glencartholm is much more diverse than that associated with *T. woodwardi*. It includes a mixture of marine and brackish water biotas with at least ten different types of malacostracans (Schram 1981a, 1983c). The sediments are interpreted as representing a transgressive sequence from coarse non-marine sandstones to marine shales (Cater *pers. comm.*). *T. etheridgii* is found in the marine shales. This subspecies is also found in a marine dolostone at Granton associated with five other malacostracan genera, plant fragments, fishes, conodont animals, myodocopid ostracodes and other invertebrates (Briggs and Clarkson 1983, Briggs, Clarkson, and Aldridge 1983, Aldridge et al 1986, Cater 1987).

This species of *Tealliocaris* was thought, by Schram (1979), to represent a species of *Pseudotealliocaris*. The features, described here, demonstrate that the similarities between *T. woodwardi* and the newly redescribed *T. etheridgii* are strong enough to place them within the same genus. The features of the abdomen are important in synonymising *Pseudotealliocaris etheridgei* with *Tealliocaris etheridgii*. The lateral expansion of the tergite of the second abdominal somite, the large third abdominal tergite which extends to cover most of the fourth, and the various oval processes of the abdomen were found to be common to all species of *Tealliocaris*.

Pseudotealliocaris was erected on the basis of specimens from Canada initially described as *Tealliocaris* by Copeland (1957). Brooks (1962, p199) was unable to obtain these Canadian specimens when he erected the new genus *Pseudotealliocaris* (Brooks 1962, p200) (see section 5.1.4). In this study it was also found that the type specimens of *Pseudotealliocaris* Brooks 1962 were too fragile to transport from Canada. Redescriptions and synonymies are therefore restricted to British specimens. However, it must be noted that the illustrations of Copeland (1957, p.44) do not show any characters that differentiate

Pseudotealliocaris from *Tealliocaris*. A high mean width to length ratio of the telson of 0.82, measured from the plates of Copeland, would suggest an affinity with *T. etheridgii.*

The large third abdominal tergite, the lateral expansion of the second abdominal tergite, as well as the oval processes on the second and third abdominal tergites, the three marked ridges of the arthrodial membrane, and the spines and ridges of the subrectangular telson on *T. woodwardi*, were found to be similar in specimens of *P. etheridgei* from Glencartholm. These similarities are sufficiently strong to justify the discontinuation of the name *Pseudotealliocaris* as applied to Scottish tealliocarids.

Tealliocaris robusta Peach 1908,
Plate 5.2a, c, d, 5.3, 5.4a; Figs. 5.8b, d, 5.9, 5.10, 5.11b.

1908 *Tealliocaris robusta* Peach. p24-25, pl.3, figs. 5-8.
1908 *Tealliocaris robusta* var Peach. p25, pl.3, figs. 9-12.
1979 *Pseudotealliocaris etheridgei* (Peach). Schram p95-99.

Lectotype.- BGS 5942 abdomen with tail fan disarticulated from carapace. Whiteadder Water, Duns, Berwickshire (Tournaisian) (Plate 5.2a).

Material.- Museum and private collections provided eleven specimens of this species from the Manse Burn Formation at Bearsden, at East Kilbride, and at Milton of Campsie, near Glasgow.

Diagnosis.- Six or seven spines on outer lateral margin of antennal scale, crenulate median keel on carapace, two transverse grooves on the third abdominal tergite.

Description.- The carapace is provided with paired post orbital spines and spines on the antero-lateral margin. Six antero-dorsal spines and an antero-ventral tubercle occur on the falcate rostrum. The pitting of the carapace of *T. robusta* is due to the epicuticle being removed, exposing the cuticular ducts of

the exocuticle. There are six to eight spines on the anterolateral margin of the antennal scale. The carapace grooves are more clearly seen in the specimens of *T. robusta*, as the preservation is better. The grooves are no different to those seen on *T. woodwardi*. A maximum of five pereiopods project laterally beyond the edges of the carapace. One specimen preserves a flagellar pereiopodal exopod. In ventral aspect, there is some sign of sternal nodes on the thorax in one specimen from Bearsden. Another ventrally exposed specimen shows crossed plates which possibly represent the lamellae or epipods, as described by Briggs and Clarkson (1985, p186) on *T. woodwardi*.

The arthrodial membrane has three marked ridges in a similar manner to the other two species of *Tealliocaris* described here. The 3rd abdominal tergite extends posterodorsally to cover most of the 4th tergite and the second abdominal somite expands laterally. Two lateral oval processes on the second and third tergite are clearly seen on most specimens. The abdominal tergites have a transverse groove on all but the 6th tergite, and the 3rd has two grooves. There are two paired pores at the posterior end of the median ridge on tergites 5 and 6. The abdominal sternites form a raised bar drawn to a median peak and connect the pleopod foramina.

The telson has two lateral spines, a crenulate median ridge with over twenty posteriorly directed spines and six spines on the postero-lateral ridges.

Remarks.- The fauna associated with *T. robusta* includes four different types of malacostracans (Wood 1982), abundant *Nucula*, rare *Modiolus* and other bivalves, and rare plant fragments. The deposit is interpreted as a mixture of marine and brackish water sediments (Wood 1982). At Duns, *T. robusta* is associated with abundant ostracodes, fishes, plants, and bivalves.

Specimens of *T. robusta* of the same age and similar preservation as specimens from Bearsden were found at East Kilbride near Glasgow and described by Peach (1908). These were identified by Peach as *T. robusta* var. Peach 1908 on the basis of being more slender and coming from a higher horizon than the type specimens of *T. robusta* from Duns. However, until evidence to the contrary is

obtained, *T.robusta* var. is synonymised with *T. robusta* (Peach 1908).

Briggs and Clarkson (1985a) observed six paired lateral spines on the rostrum of *T. woodwardi*. This differs from the description of the rostrum of *T. robusta* presented here. On compaction, the falcate rostrum may give the impression of having lateral spines. The rostrum is also significantly longer than in *T. woodwardi* or *T. etheridgii*. The sternal nodes which may be present on the thoracic sternites of *T. robusta* have not been recorded on any other tealliocarid except *T. woodwardi*. This may be due to the small number of specimens, of the other species, preserved to show the sternum.

The oval processes on the second and third abdominal tergite present on *T.woodwardi* and *T. etheridgii* are less pronounced than those of *T. robusta* probably as a result of the preservation.

General remarks on *Tealliocaris*.- *Tealliocaris* is one of the more familiar shrimps in the fossil crustacean faunas of the Carboniferous of central and southern Scotland. These faunas are commonly associated with fish, bivalves, and plants in facies which have been variously interpreted as marginal marine, brackish, lagoonal, hypersaline and freshwater in origin (Dewey and Fåhræus 1982, Briggs and Clarkson 1983, 1985a, Hesselbo and Trewin 1984, Cater 1987). *Tealliocaris* is also one of the best preserved and one of the most widespread of Carboniferous crustaceans. It has been recorded from France (Carpentier 1913) northern England and southern Scotland (Peach 1908, Schram 1979) and Canada (Dewey and Fåhræus 1982).

Peach (1908, p16) indicated that "the structure of the endopodites of all these limbs (thoracopods) seems to fit them better to form a great restraining apparatus for the entrapping of minute organisms rather than for crawling or swimming". The morphology of the limbs does seem to support Peach's statement, and because of the similarity between the thoracic limbs of *Procaris* and those of *Tealliocaris*, they may have had similar feeding habits. *Procaris* occasionally uses its pereiopods to catch prey, such as the atyid *Typhlatya rogersi* using its pedeform maxillipeds to manipulate the prey

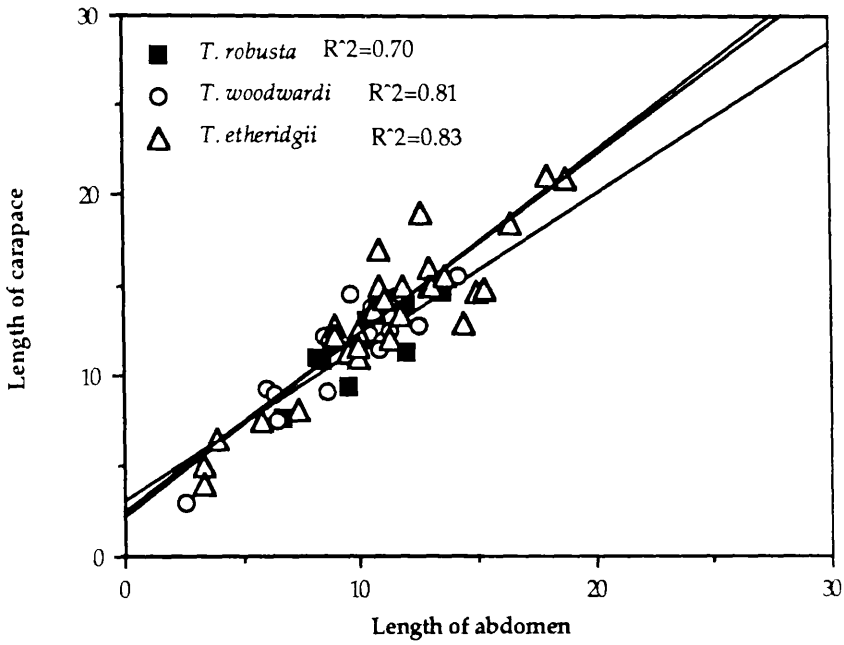
close to the mouth parts while it swims upside down using its flagelliform pereiopodal exopods and pleopods (Provenzano 1978, p171, Abele and Felgenhauer 1985, p20). The massive mandibles are used both to tear at prey and, more commonly, to feed on algae and diatoms.

The lack of any associated fauna on which *T. woodwardi* could actively prey does not preclude the possibility of similar feeding habits to those of *Procaris*. Briggs and Clarkson (1985a, p200) suggested that *T. woodwardi* could have been a detritus feeder, as well as a filter feeder. *T. etheridgii* has a large and varied associated faunal assemblage and may have used its limbs for grasping crustaceans such as *Crangopsis*. *T. robusta* may also have fed in this manner although the faunal assemblage is less varied.

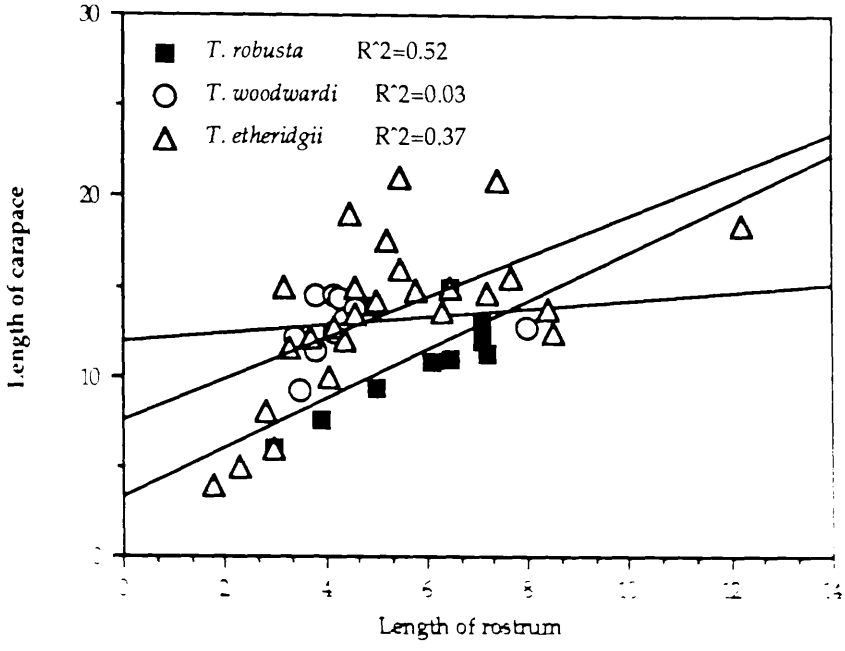
Peach differentiated between his species of *Tealliocaris* on the keels on the carapace and the abdomen as well as the relative length of the tails to total length. Many of the characters used by Peach (1908) may differ purely as a result of preservation and collecting bias. However, the characters, both morphological and morphometric, used here, to differentiate between the two species of *Tealliocaris*, are not affected by the state of preservation. These characters, such as the number of spines on the anterolateral margin of the antennal scale and the presence of spines on the anterolateral margin of the carapace, are consistent within each locality. The values of the ratio of the width of the telson to its length (wt/lt) and the length of the rostrum (lr/lc) vary within each locality and show some overlap with values from other localities. Statistical t-tests on these ratios show that there is a significant difference between *T. etheridgii* and the other forms of *Tealliocaris* although, the small number of specimens available makes the interpretation less reliable.

Figure 5.6 Graphs showing the relative proportions of the length of the telson (lt), width of the telson (wt), length of the carapace (lc), abdominal length (la), and the length of the rostrum (lr) in the different species of *Tealliocaris*. a) lc/la; b) lc/lr; c) lt/wt. (measured in mm).

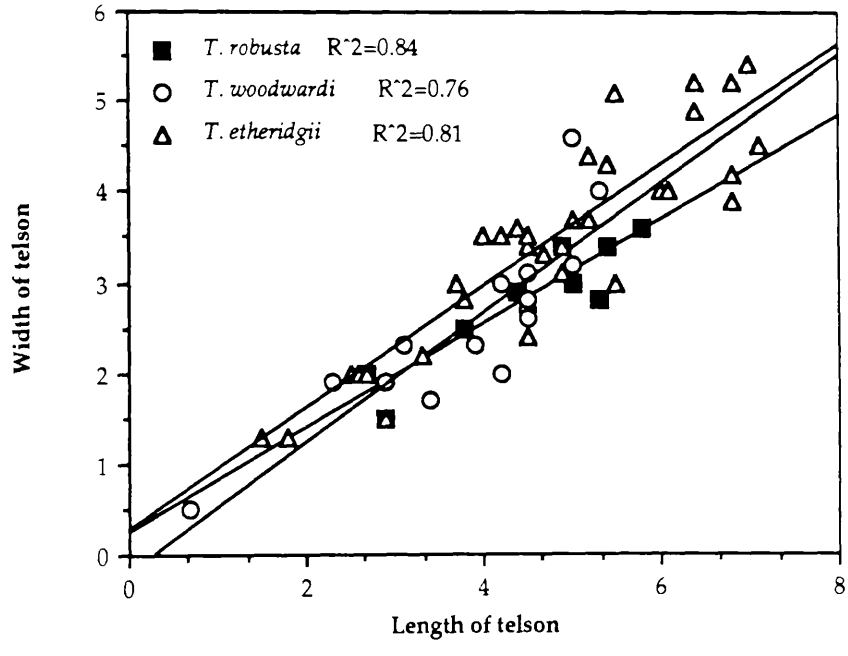
a)



b)


T. robusta R^2=0.52
T. woodwardi R^2=0.03
T. etheridgii R^2=0.37
Length of carapace
Length of rostrum

c)


T. robusta R^2=0.84
T. woodwardi R^2=0.76
T. etheridgii R^2=0.81
Width of telson
Length of telson

The reason for the new diagnostic characteristics not being observed previously is purely a result of the preservation and preparation of specimens. Few external moulds of *T. woodwardi* have previously been studied as the specimens tend to fracture internally (Briggs and Clarkson, 1985a), and Glencartholm specimens are variably altered or damaged during preparation. It is, therefore, not surprising that many of the structures seen on *T. robusta* from Bearsden were not previously recorded.

It is possible that some of the differences between the species are ecophenotypic, as they occur in two different environments. *T. woodwardi* has only been found in restricted fresh, brackish, or hypersaline bodies of water with a paucity of associated faunal elements. Whereas, *T. etheridgii* and *T. robusta* occur in a more marine setting with a with a wide range of associated brackish and marine faunas. As the differences stated are consistent between localities, it is suggested that the forms of *Tealliocaris* should be considered as separate species.

The carapace of *Tealliocaris* has many characters which are comparable with extant decapods. It extends to cover the thorax completely and may have been attached dorsally to the abdomen via the arthrodial membrane. The dislocation of the carapace with respect to the abdomen probably represents a moult.

Only five of the eight achelate pedeform thoracic limbs extend laterally beyond the margin of the carapace. The anterior two limbs are pedeform, project anteriorly and are interpreted as maxillipeds. Attached to the posterior five thoracic limbs are flagellar pereiopodal exopods and epipods. These are similar in character to those of the extant decapod *Procaris* (Chace and Manning 1972).

Due to the dislocation of the cephalothorax from the abdomen seen in the majority of specimens, the thorax has previously been assumed to be unattached to the carapace. Briggs and Clarkson (1985a, p174) suggested that this may be as a result of moulting. Only those specimens with gut traces preserved can be

Plate 5.2

a) Lectotype of *Tealliocaris robusta* from the Whiteadder Water, Berwickshire (BGSE 5942; X4.2).

b) Lectotype of *Tealliocaris etheridgii* from Glencartholm, near Langholm (BGSE 5918; X3.25).

c) *Tealliocaris robusta* from the Shrimp Member at Bearsden (UCZ I.9430; X4). Arrow points to the third abdominal somite.

d) *Tealliocaris robusta* from Bearsden with arrow showing the pereiopodal exopod (HM A2405b; X11).

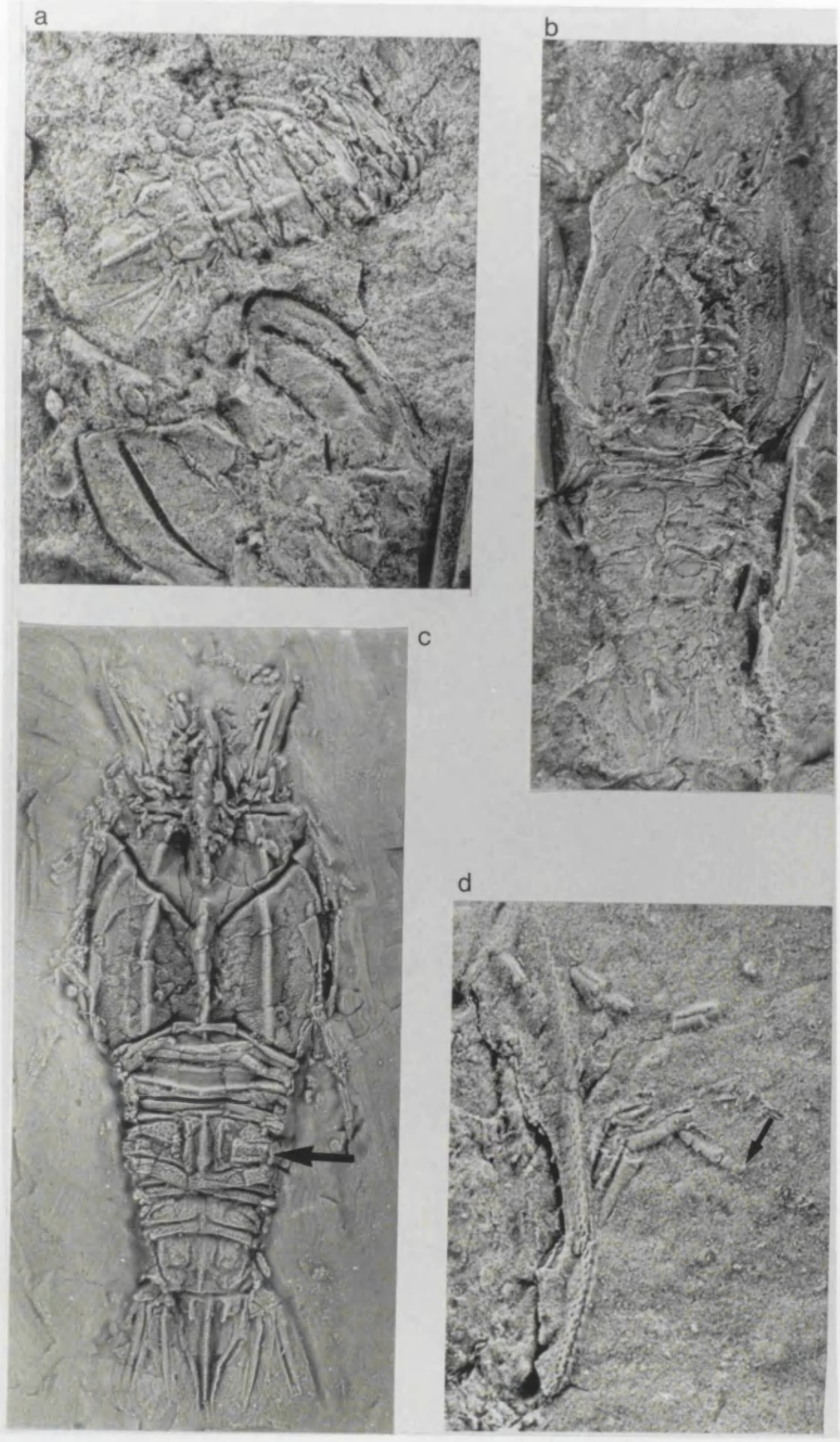

a
b
c
d

Plate 5.3

Tealliocaris robusta from Bearsden with arrow pointing towards the thoracic lamellae (HM A2407b; X5).

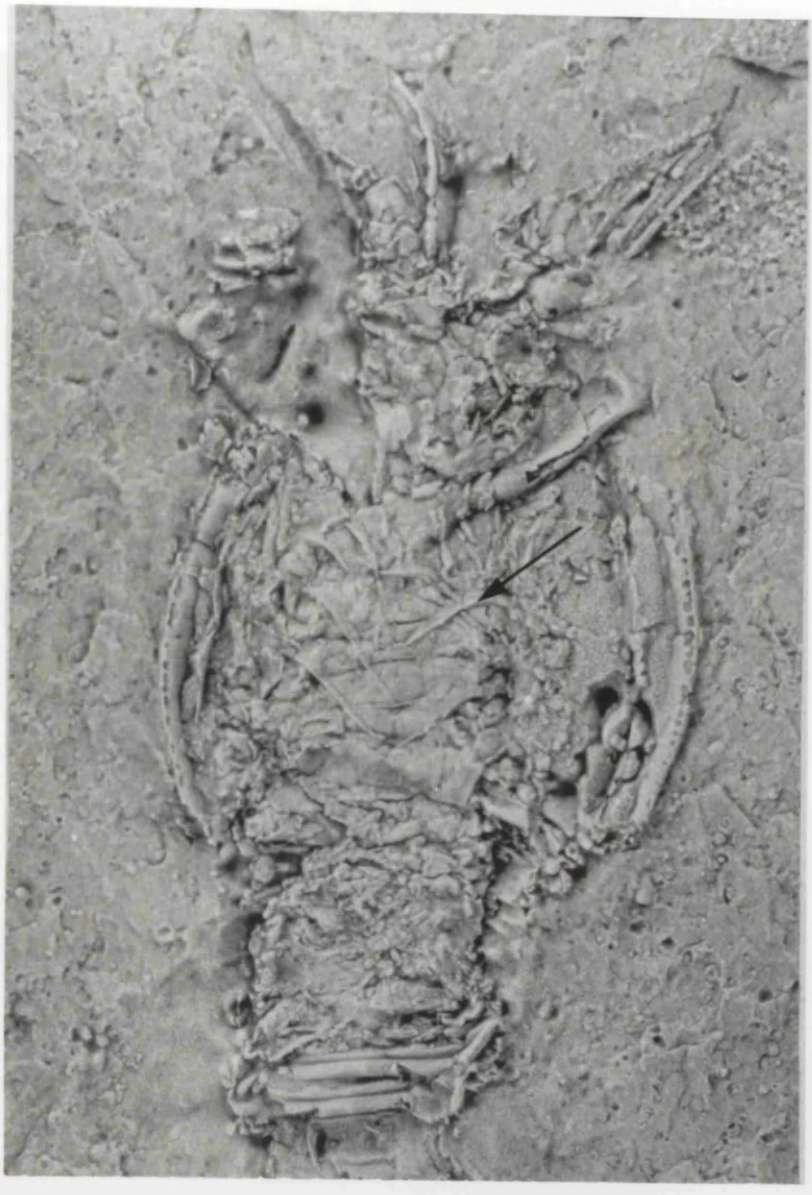


Plate 5.4

a) *Tealliocaris robusta* from Bearsden with arrow pointing to muscle blocks within the abdominal cavity (HM A2408; X4.8).

b) *Tealliocaris etheridgii* from Glencartholm showing lateral aspect with arrow pointing to the second abdominal pleuron (BGS 5917; X5.5).

c) *Tealliocaris woodwardi* from Gullane showing anterior limbs (HM A2388-1; X5.5).

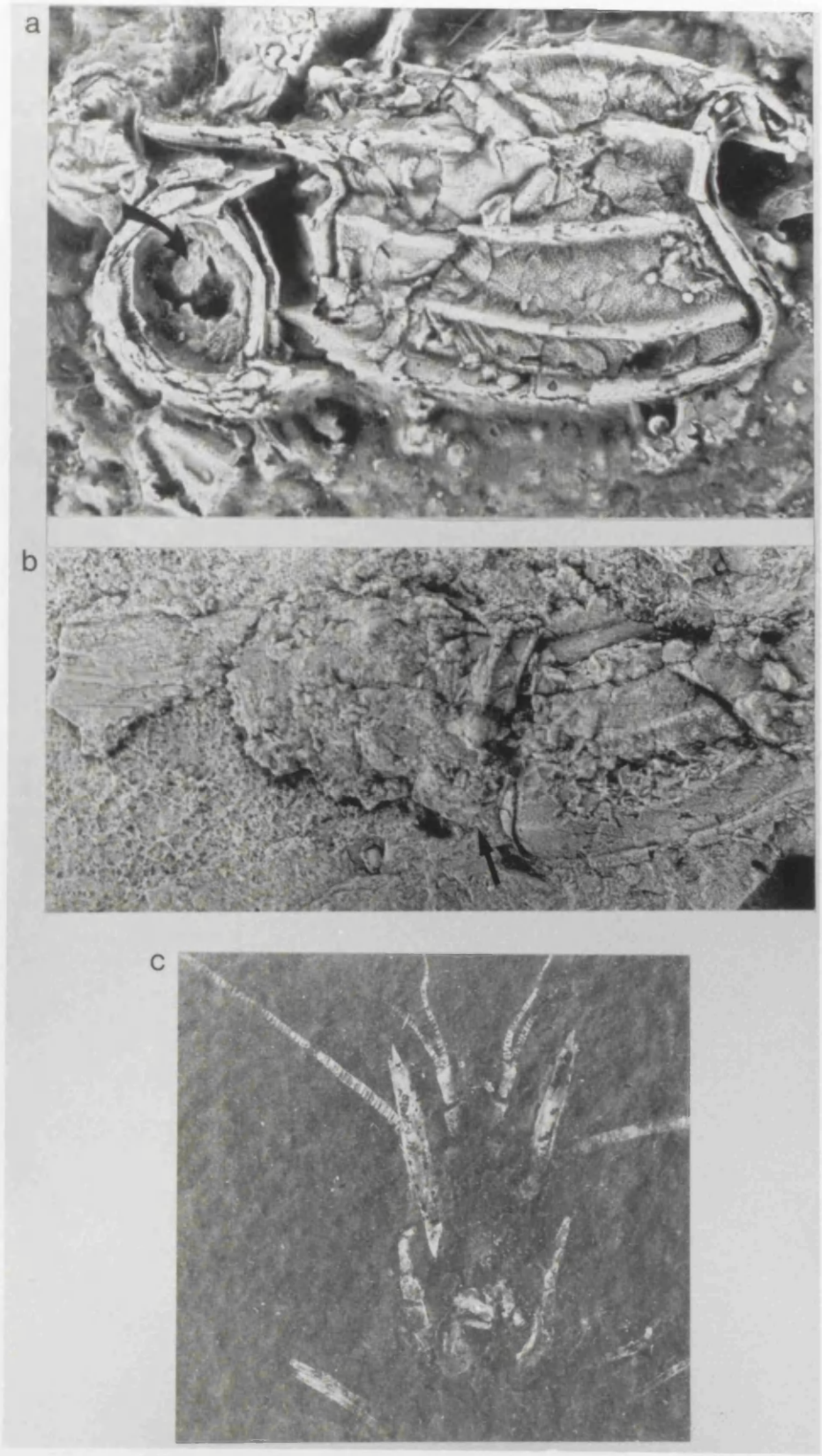

a
b
c

Plate 5.5

a) *Tealliocaris woodwardi* from Gullane showing dorsal aspect with arrow pointing to the third abdominal somite (HM A3289a; X4.25).

b) Ventral view of the above specimen (HM A3289b; X4.25).

c) *Tealliocaris etheridgii* from Glencartholm with arrow pointing to the third abdominal somite (BM 138022; X2).

d) Highly magnified telson of *Tealliocaris woodwardi* from Gullane (HM A21507; X32.5).


a
b
c
d

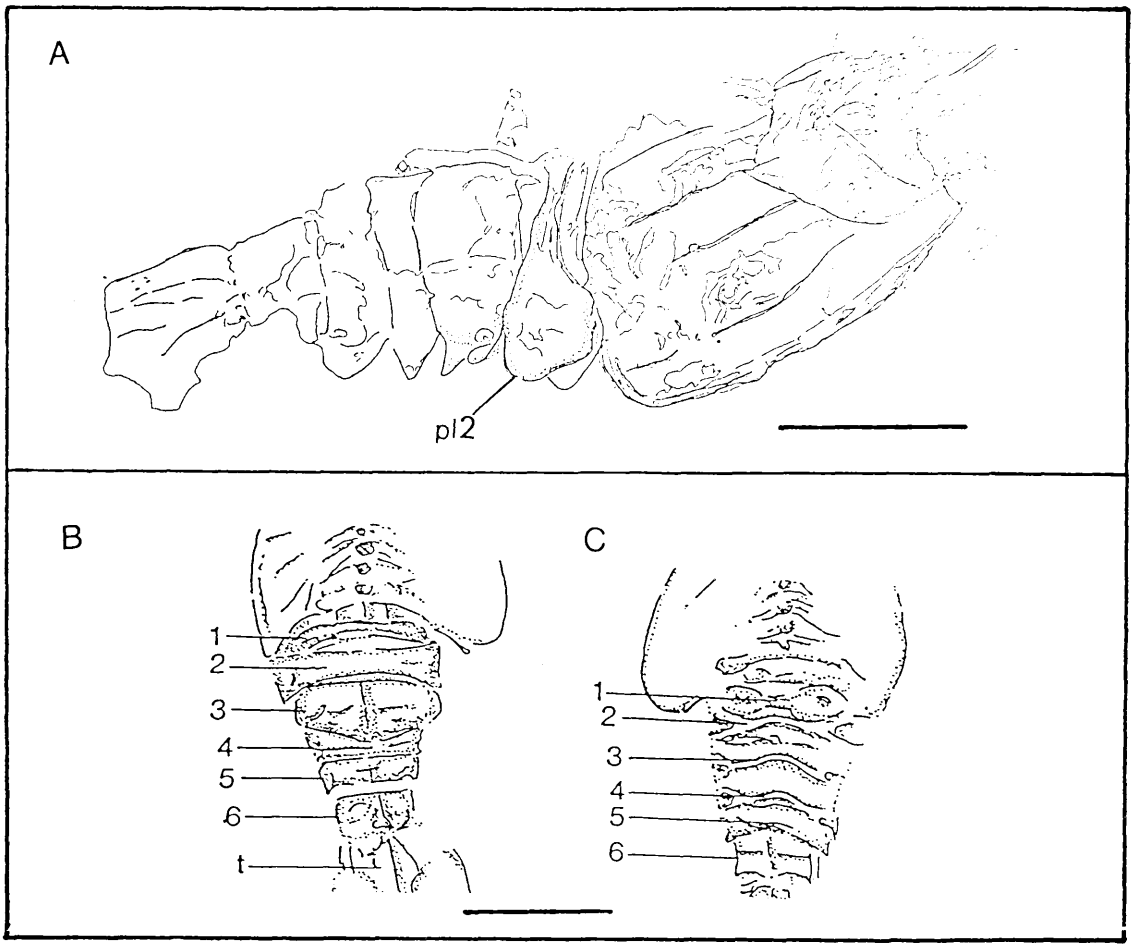


Figure 5.7

a) *Tealliocaris etheridgii* in lateral view (BGSE 5917; scale-bar = 0.5cm). pl2=second abdominal pleuron.

b) *Tealliocaris woodwardi* in dorsal view (HM A3289a; scale-bar = 0.5cm). 1-6=abdominal somites, t=telson.

c) *Tealliocaris woodwardi* in ventral view (HM A2389b; scale-bar = as 'b' above). 1-6=abdominal somites.

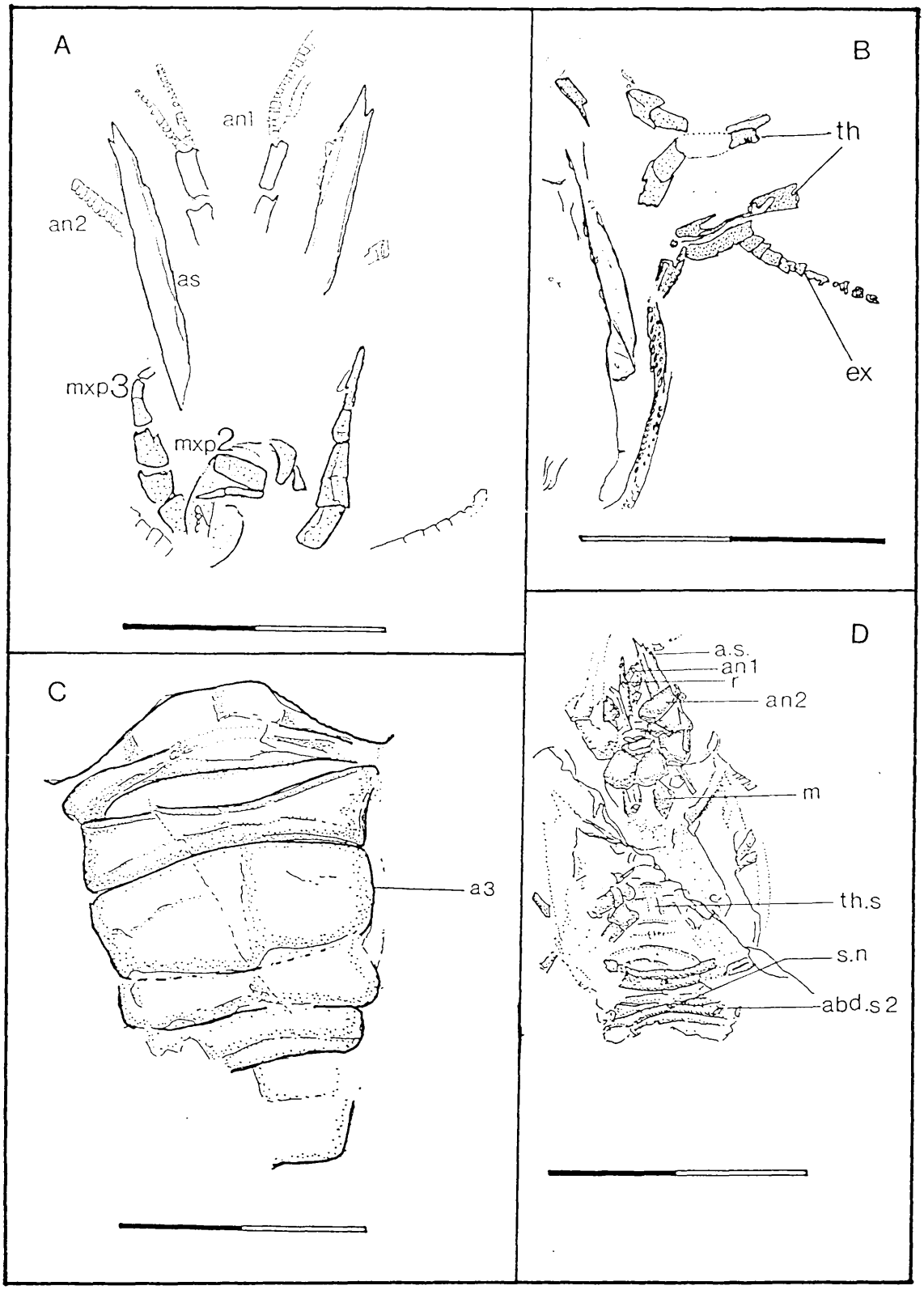
Figure 5.8

a) *Tealliocaris woodwardi* showing anterior limbs (HM A2388-1; scale-bar = 0.5cm). an1=first antenna, an2=second antenna, as=antennal scale, mxp2=second maxilliped, mxp3=third maxilliped.

b) *Tealliocaris robusta* showing pereiopodal exopod (HM A2405b; scale-bar = 0.5cm). th=thoracopods, ex=exopod.

c) Abdomen of *Tealliocaris etheridgii* (BM 138022; scale-bar = 0.75cm). a3=third abdominal somite.

d) Ventral view of *Tealliocaris robusta* (HM A2405a; scale-bar = 1cm). a.s.=antennal scale, an1=first antenna, an2=second antenna, r=rostrum, m=mandibles, th.s=thoracic sternites, s.n=sternal node, abd.s2=second abdominal sternite.


A
an1
an2
as
mxp3
mxp2
B
th
ex
C
a3
D
a.s.
an1
r
an2
m
th.s
s.n
abd.s 2

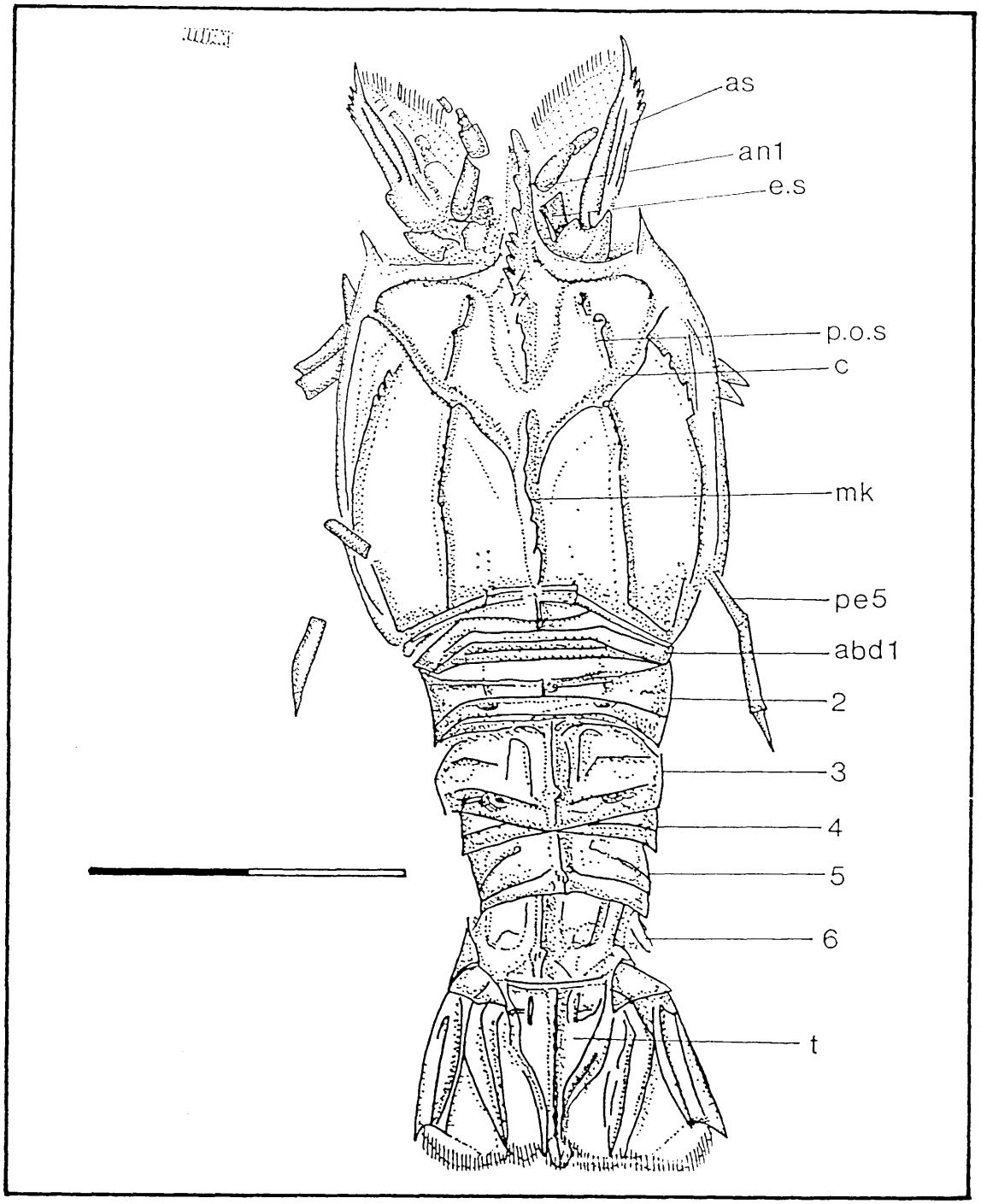


Figure 5.9

Line drawing of *Tealliocaris robusta* (UCZ I.9430; scale-bar=1cm). as=antennal scale, an1=first antenna, e.s=eye stalk, c=cervical groove, p.o.s=post orbital spines, mk=median keel, pe5=fifth thoracopod (pereiopod), abd1-6=abdominal somites, t=telson.

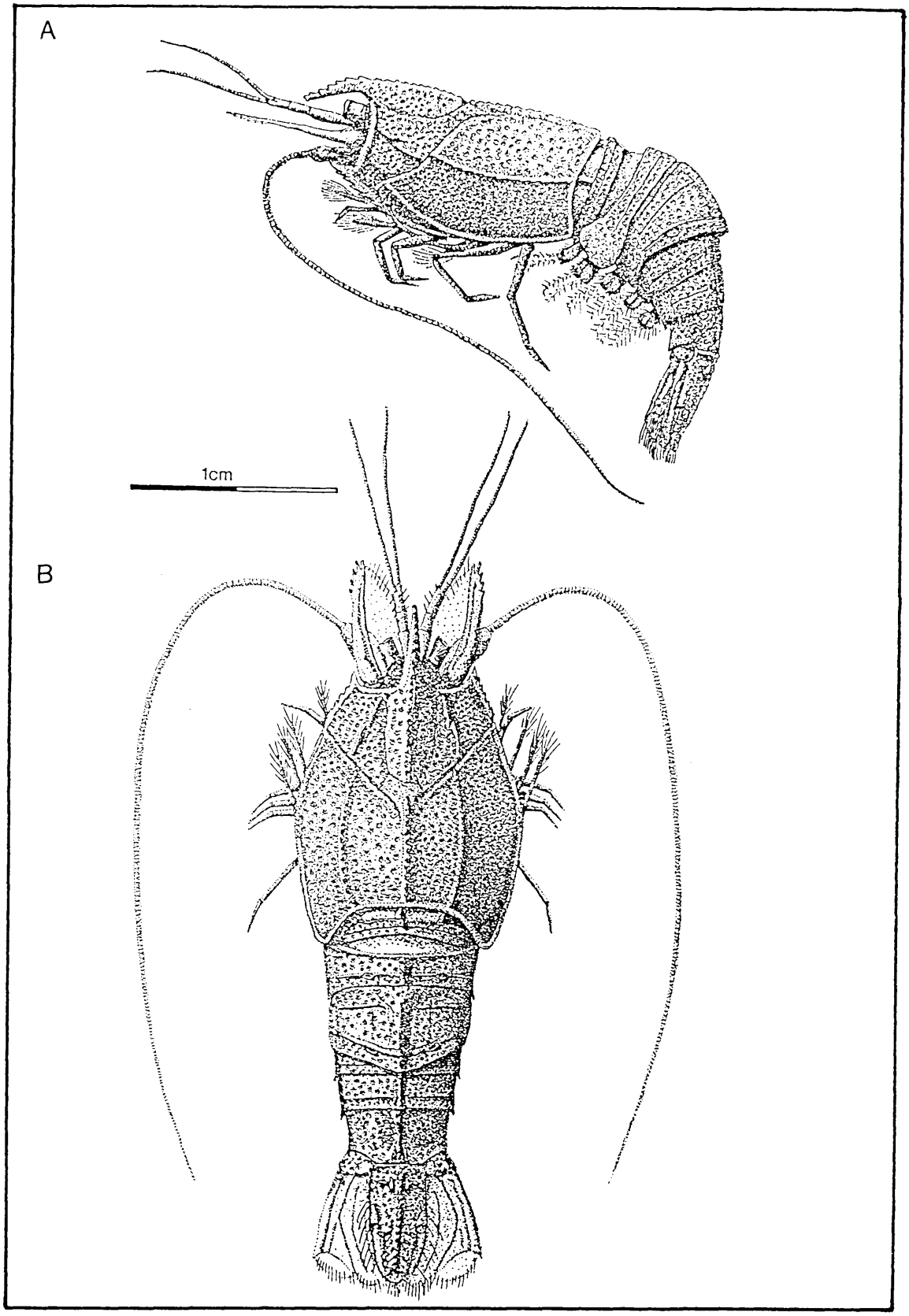


Figure 5.10

a) Lateral reconstruction of *Tealliocaris robusta*.

b) Dorsal reconstruction of *Tealliocaris robusta*.

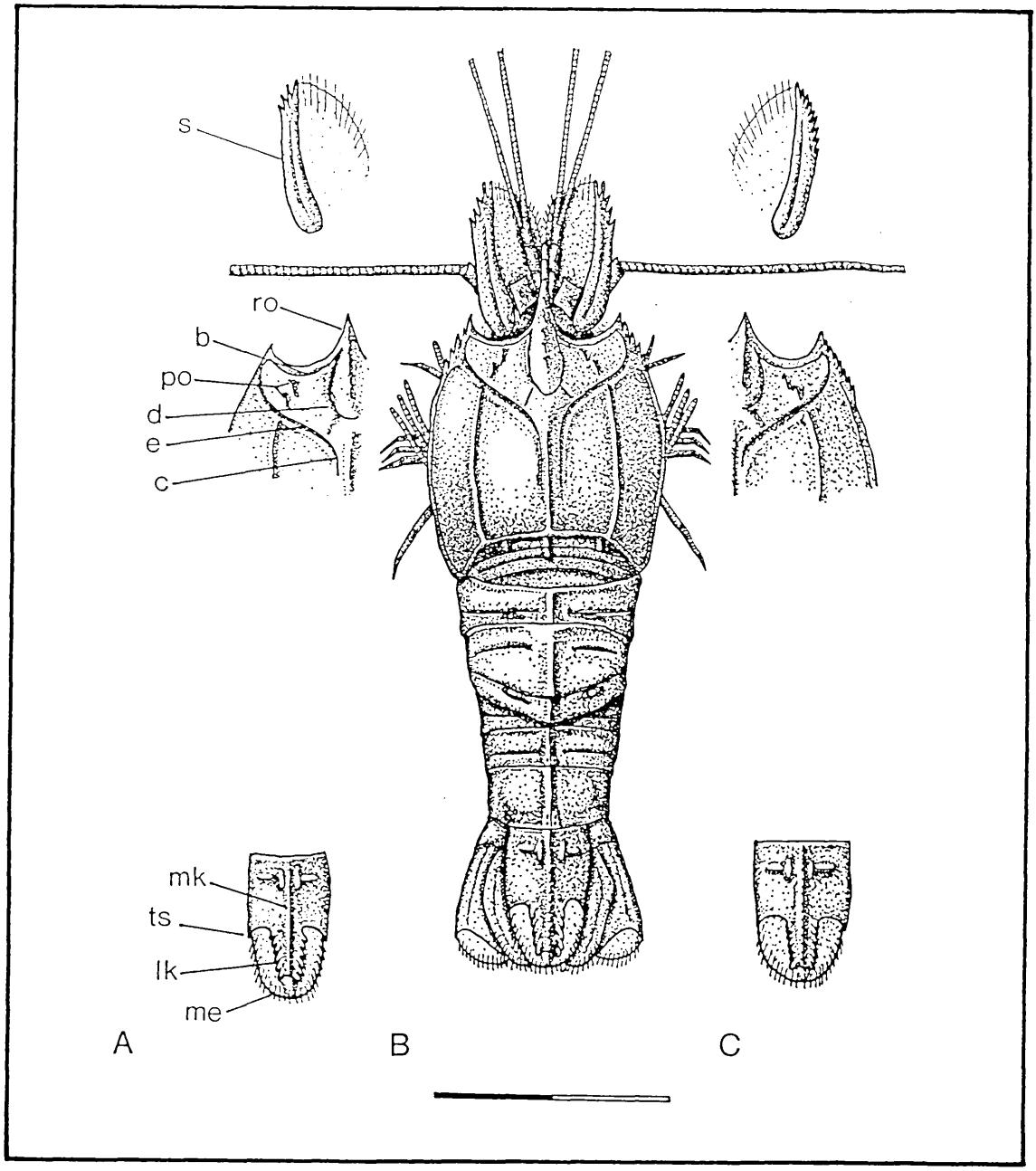


Figure 5.11

a) Characteristic features of *Tealliocaris woodwardi.*

b) Characteristic features of *Tealliocaris robusta.*

c) Characteristic features of *Tealliocaris etheridgii.*

scale-bar=1cm, s=antennal scale, ro=rostrum, b,d,e,c=carapace grooves, po=post orbital spines, mk=median keel, ts=telson spine, lk=lateral keel, me=membrane.

considered as true corpses.

The detailed taxonomy of *Tealliocaris*, as well as its position within the Crustacea have been likewise subject to numerous and inconsistent interpretations during the history of research into the genus. Evidence presented here indicates that *Tealliocaris* is a representative of the most primitive form of decapods.

Order Eocarida Brooks 1962

Genus *Crangopsis* Salter 1863

Type species.- *Uronectes socialis* Salter 1861 from Ardross, Fifeshire, Calciferous Sandstone Measures (Lower Carboniferous).

Diagnosis (after Schram 1979, p39).- Carapace subtrapezoidal. Antennal peduncles moderately large and long. Abdomen 2.5 times the length of the cephalothorax. Sixth abdominal somite especially elongate. Pleuron of the second abdominal somite extends markedly anteriad as well as posteriad.

Crangopsis eskdalensis (Peach) 1882.

Plate 5.6a-d; Figs. 5.14a-d, 5.15a-c, 5.16.

1882 *Palaeocrangon eskdalensis* Peach, p84, pl.8, fig.9.

1908 *Crangopsis couttsi* Peach. p76-78, pl.12, figs. 1-7.

1908 *Crangopsis eskdalensis* (Peach). Peach, p80-81, pl.11, figs. 1-7.

1969 *Crangopsis eskdalensis* (Peach). Brooks, p343, fig. 158, 6.

1979 *Crangopsis eskdalensis* (Peach). Schram, p42-45, figs. 9, 11.

Lectotype.- BGS 5007 from Glencartholm, near Langholm. Calciferous Sandstone Measures (Lower Carboniferous).

Diagnosis (after Schram 1979, p43).- Carapace rounded on postero-ventral

corner. Second abdominal pleuron flattened ventrally. Posterior abdominal pleura rounded on postero-ventral corners.

Material.- The specimens obtained from Bearsden occur abundantly at two levels: 1) within the Shrimp Member (Bed A of Wood 1982) and, 2) a thin horizon within the Lingula Member (Bed E of Wood 1982). This crustacean is the most abundant component of the fauna at Bearsden and the other localities where the Shrimp Member is present.

Description.- The specimens of *Crangopsis eskdalensis* from the Shrimp Member are mostly incompletely preserved. The carapace and abdomen are usually well preserved, and the tail fan and appendages, less so, or not at all preserved. Where the shrimps have been replaced by secondary drusy calcite, however, the outline of the tail fan can be distinguished although much of the finer detail is lost.

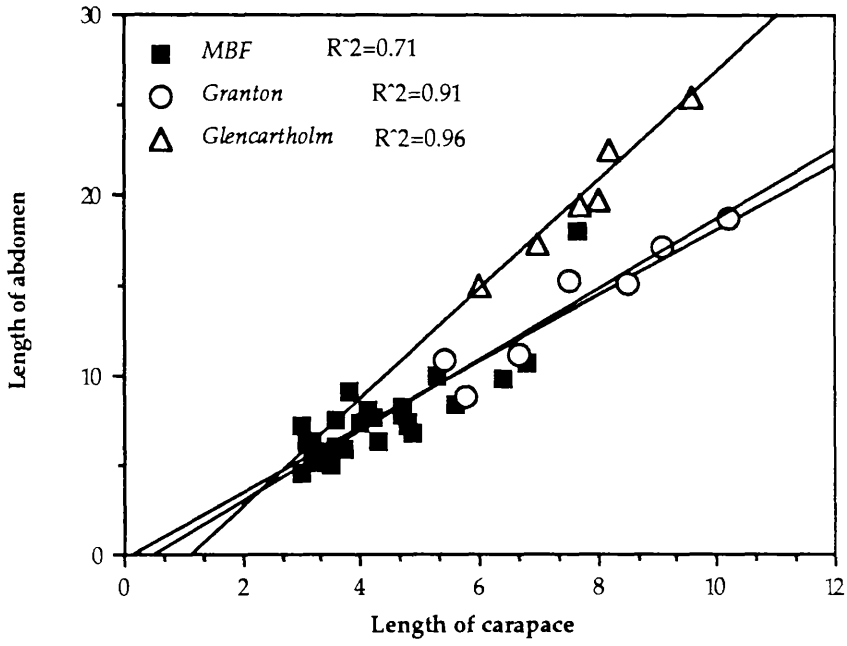
The carapace is subtrapezoidal to triangular with only a very slight rostrum projecting anterior to the transverse cervical groove. The cervical groove is indistinct due to crushing and wrinkling of the thin cuticle. The antennal peduncles are quite large relative to those seen in other Carboniferous genera. No specimens from the Manse Burn Formation are preserved showing the full extent of the first antennae. The basal segments of the second antennae are short. The distal segments of the second antennae are poorly preserved and indistinct. The antennal scale is sometimes preserved as an oval plate at least as long as the first peduncle of the antennules. The carapace is medially incised to reveal at least two of the thoracic somites. Where the carapace has been totally removed, at least four short thoracic segments are clearly visible in lateral aspect (see Fig. 5.14b). This suggests that the carapace was not fully attached to the thorax in life. The thoracopods are poorly preserved in all specimens collected, although at least seven can be seen in one specimen (see Fig. 5.15c).

The abdomen is nearly three times the length of the cephalothorax with the sixth abdominal somite approximately 0.75 times the length of the carapace.

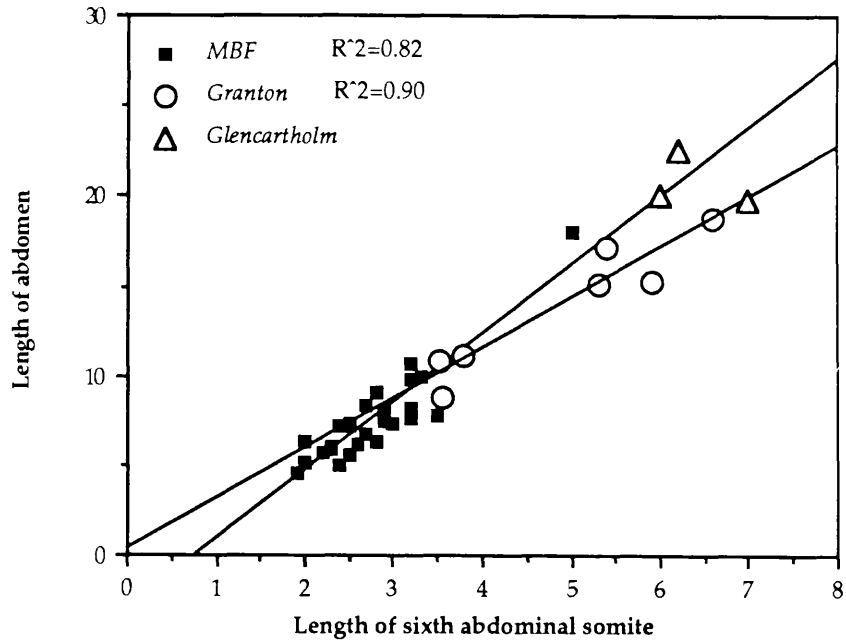
The pleura of the abdominal somites 1, 3, 4, and 5, are rounded posteriorly and overlap the pleura of the next posterior somite. The pleura of the second abdominal somites are subrectangular with a flattened ventral margin. The cuticle of *Crangopsis eskdalensis* is largely smooth, with only the fine pitting of the tegumental ducts visible at high magnification. On the tergite of the second abdominal somite, however, there is a small boss with a median slit, which presumably represents a sensory device.

Figure 5.12 Graphs showing the relative lengths of the carapace (lc), abdomen (la), and the sixth abdominal somite (la6) in *Crangopsis* from different localities (MBF=Manse Burn Formation). a) la/lc; b) la/la6. (measured in mm).

a)



b)



The tail fan is poorly preserved, but appears to consist of a triangular to sub-rectangular telson, approximately equal in length to the uropodal exopod. The uropodal exopod is longer than the endopod, and appears to have an outwardly concave margin.

Remarks.- The presence of *C. eskdalensis* north of the Southern Uplands suggests that the western Midland Valley of Scotland had more contact with the Northumberland Trough, than with the eastern Midland Valley where *C. socialis* was dominant during the Viséan (Schram 1979). The palaeogeography and palaeogeomorphology of the Midland Valley during the early Namurian would suggest an eastward transport of these crustaceans from Ireland. However, no crustaceans of this genus have, so far, been recorded from the Irish Namurian.

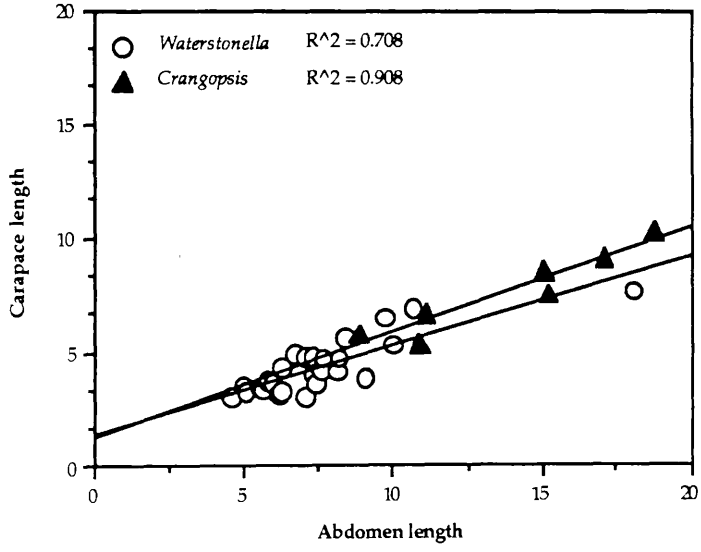
The few new structures which have been observed on *C. eskdalensis* include: 1) at least four thoracomeres free of the carapace, of which the posterior two can be seen in the deeply incised medial portion of the posterior margin of the

carapace; 2) the presence of a sensory device on the second abdominal somite; 3) the presence of *C. eskdalensis* north of the Southern Uplands.

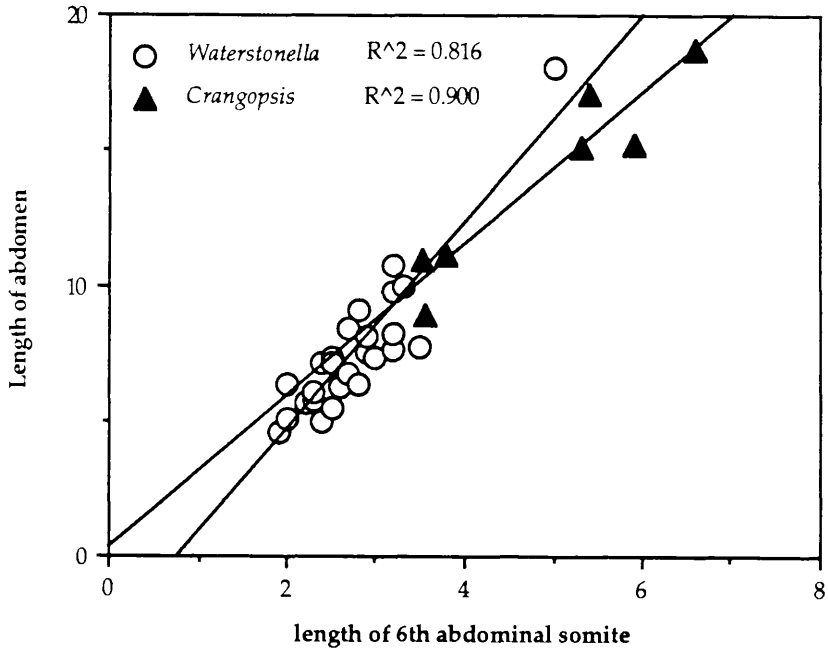
A difficulty in differentiating between specimens of *Crangopsis* socialis and *Waterstonella* from the Granton Shrimp Bed, near Edinburgh, arises due to the range and style of preservation. It is possible to observe a full range of morphologies from the thicker *Crangopsis* morphology, to the thin *Waterstonella* morphology. The major differences between these morphologies includes the preservation of the thoracopods,and the preservation of the large second abdominal pleura. In *Waterstonella* there are ten thoracopods of which the anterior two are shorter than the other eight, several of the thoracic somites are free of the carapace (Briggs *et al. in prep.*), and the relative proportions of the sixth abdominal somite, the carapace, and the abdomen are the much the same between the *Crangopsis* and *Waterstonella* morphologies.

Figure 5.13 The relationship between: a) the length of the carapace and the abdomen, b) the length of the abdomen and the 6th abdominal somite, and c) the length of the uropodal exopod and the abdomen of *Waterstonella* and *Crangopsis* from the Granton Shrimp Bed, near Edinburgh.(measured in mm).

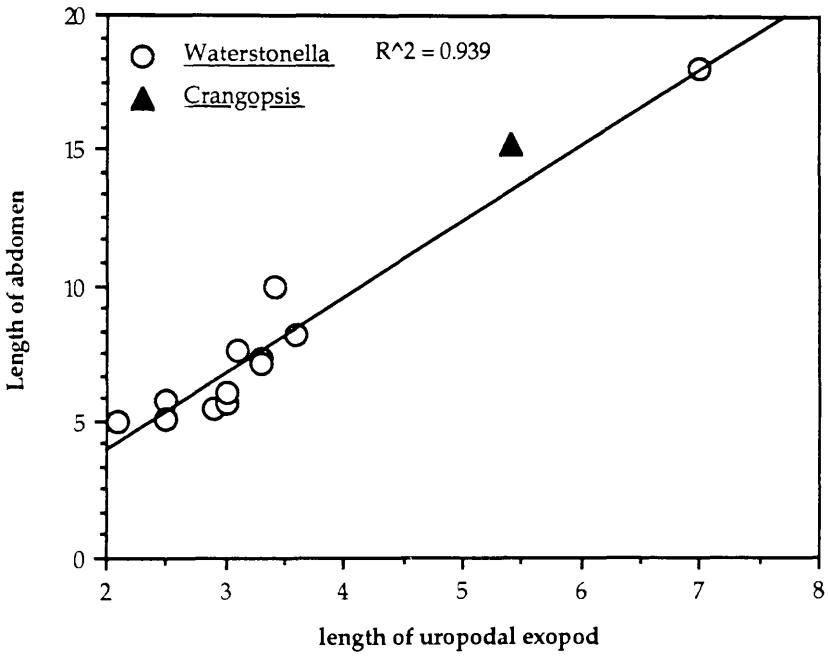
a)



b)



c)



One specimen classified as *Crangopsis* by Briggs and Clarkson (1983, pl.22,

fig7) has the same number of thoracic limbs as *Waterstonella* and yet has all the features of *Crangopsis*, such as the large pleura of the second abdominal somite. It seems as though the pleura of the abdomen do not preserve well, whereas the thoracopods do. This may be due to several moult stages being preserved, although it is unclear why the limbs should be poorly preserved where the carapace and the abdomen are well preserved (*Crangopsis* morphology). *Waterstonella* and *Crangopsis* are thus held to be coterminous and thus *Waterstonella* is a synonym of *Crangopsis*.

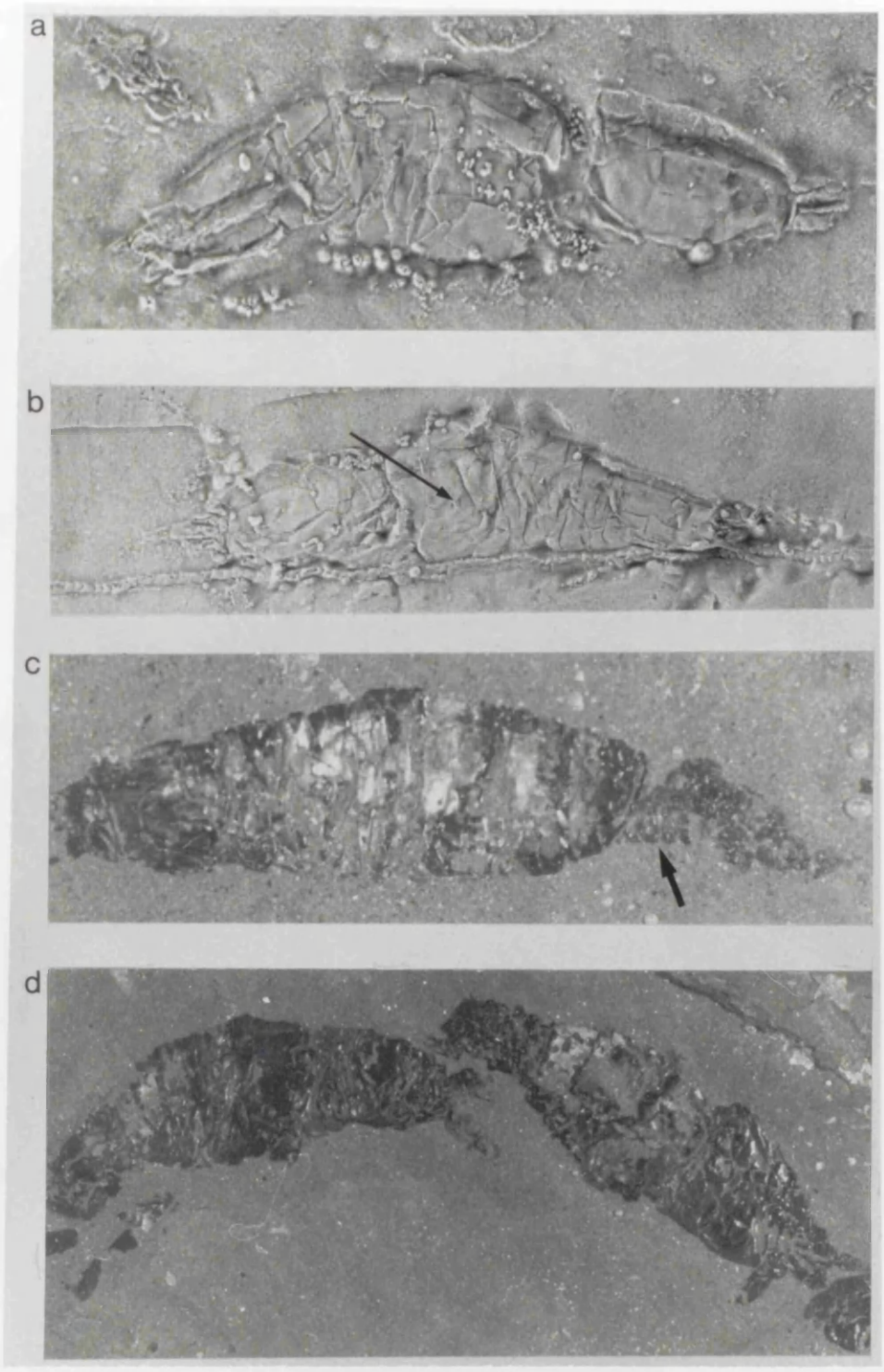
Plate 5.6

a)*Crangopsis eskdalensis* from the Shrimp Member at Bearsden (HM; X5).

b)*Crangopsis eskdalensis* from the Shrimp Member at Bearsden associated with the antenna of *Palaemysis* (HM A2409/8; X5). The arrow points to the small boss on the second abdominal pleuron.

c)*Crangopsis eskdalensis* from the Shrimp Member at Bearsden showing the thoracic somites (HM A2409/6; X5). Photographed in water.

d) *Crangopsis eskdalensis* from the Shrimp Member at Bearsden (HM A2409/9; X4). Photographed in water.


a
b
c
d

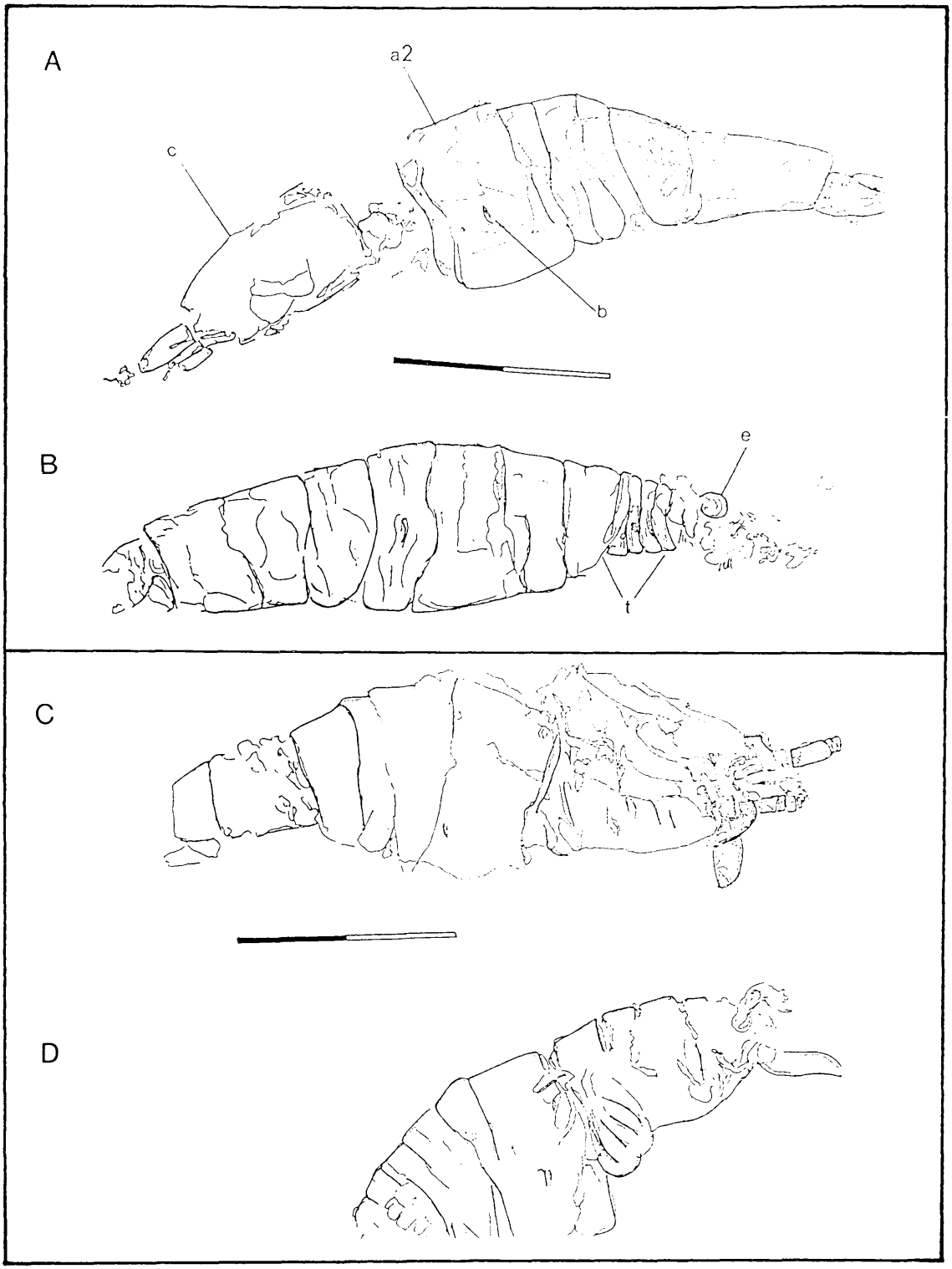


Figure 5.14

a) *Crangopsis eskdalensis* (HM A2409/8; scale-bar=0.5cm). c=carapace, a2=second abdominal somite, b=boss.

b) *Crangopsis eskdalensis* (HM A2409/6; scale-bar=as above). e=eye, t=thoracic somites.

c & d) *Crangopsis eskdalensis* (HM A2409/9 [same block]; scale-bar=0.5cm).

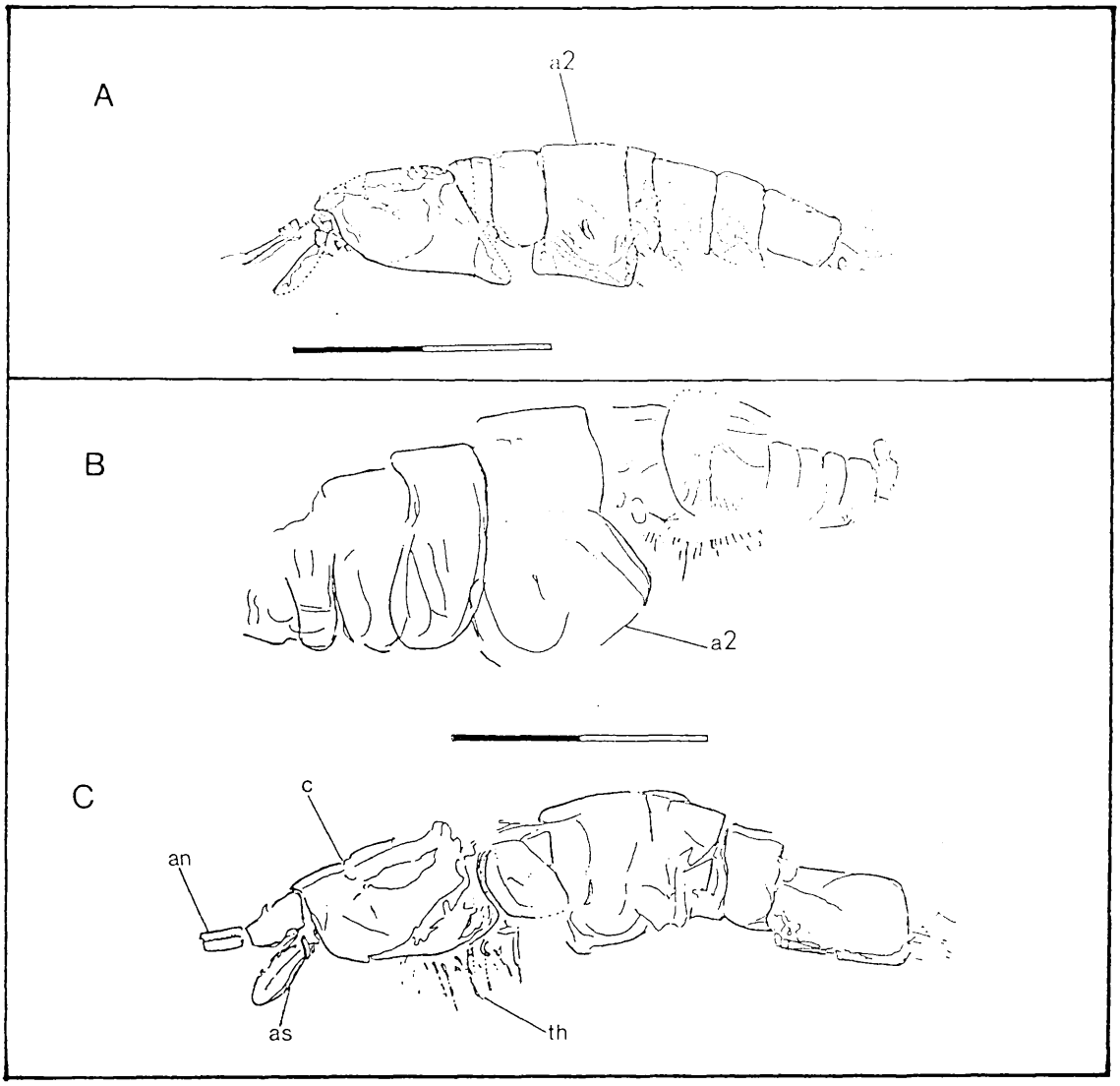


Figure 5.15

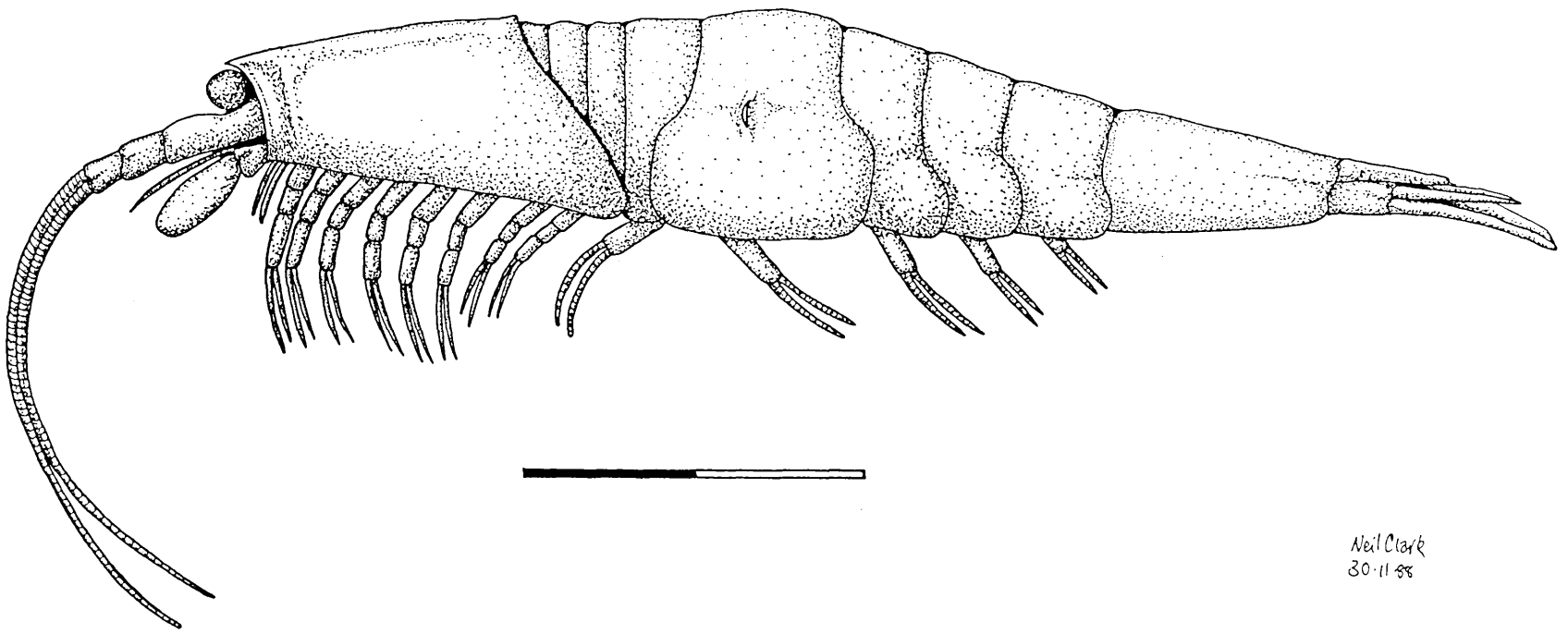
a) *Crangopsis eskdalensis* (HM A2409/1; scale-bar=0.5cm). a2=second abdominal somite.

b) *Crangopsis eskdalensis* (HM A2409/4; scale-bar=0.5cm). a2=second abdominal somite.

c) *Crangopsis eskdalensis* (HM A2409/5; scale-bar=as above). an=antennae, c=carapace, as=antennal scale, th=thoracopods.

Figure 5.16

Reconstruction of *Crangopsis eskdalensis* (scale-bar≈0.5cm).



Genus *Palaemysis* Peach 1908

Type species.- *Palaemysis dunlopi* Peach 1908

Diagnosis.- Carapace laterally triangular, anterior flagelliform spinose appendage, seven pairs of thoracic endopods with flagellar distal ends, second abdominal pleura overlap those of the first and third, rectangular telson with median groove, exopodal uropod blade-like with diaeresis.

Palaemysis dunlopi Peach 1908

Plate 5.7b, c, 5.8a-c, 5.9a-f; Figs. 5.18a-e, 5.19a, 5.20a-e, 5.21a-e, 5.22a-c.

1908 *Palaemysis dunlopi* Peach. p57-59, pl.8, figs. 12-14.

1908 *Palaemysis couttsi* Peach. p59, pl.8, figs. 16-19.

1908 *Palaemysis tenuis* Peach. p60, pl.8, figs. 20-24.

1908 *Palaemysis sp.* Peach. p60, pl.8, fig. 25.

1969 *Anthracophausia dunsiana* Peach, 1908. Brooks. p342-343.

1979 *Anthracophausia dunsiana* Peach, 1908. Schram. p67-72.

1982 *Anthracophausia sp.* Wood. p576, fig. 4.

1983 *Anthracophausia dunsiana* Peach, 1908. Briggs and Clarkson. p165, 170, figs. 3, pl.20, figs. 2-6.

1985 *Anthracophausia dunsiana* Peach, 1908. Clarkson. p12-13, figs. 4-5.

1986 *Anthracophausia sp.* Schram. p106, fig. 9-3.

Type.- BGS 5868 (T2769) (Peach 1908; pl 8, fig 12) tail fan and abdomen from Greengairs, Airdrie, near Glasgow (Lower Coal Measures, Westphalian A).

Diagnosis.- As only one species is recognised, the diagnosis for the species is the same as for the genus.

Description.- The cuticle is thin with a fine external microreticulate surface texture. The rostrum is short and the laterally triangular carapace has a weak straight cervical groove. The carapace extends to partially cover the thorax

although dorsally the carapace is excavated deeply and may partially expose the eighth thoracic tergite. Eye stalks are long and appear to originate on or near the first segment of the antennules. The antennules are biramous with three proximal segments, the most distal of these being shorter and circular, and giving rise to two multi-articulate flagellae. The antennal scale is about a fifth of the total length and has an outer lateral fringe, and an inner lateral margin of robust bifurcating setae. The antennal flagellum is shorter than the antennal scale and is rarely seen except on a few exceptional specimens. A pair of rounded limbs with long, sharp spines near the base of the frontal appendages may represent the endopods of the maxillae. The most striking feature of this shrimp are the spinose frontal appendages which consist of two proximal segments and twelve distal segments each with a pair of spines. These appendages are about half the total body length. Of the specimens from the Shrimp Member which have the anterior spinose appendage preserved, 71.8% do not have the distal segments folded. Of the other specimens, 20.52% break at either the third or fourth segment from the distal end. This may be due to a weakening of the joints during moulting and the way the moult comes to rest on the substrate surface. This pair of limbs was previously thought to represent the second antennal flagella (Wood 1982), however, this cannot be so, as the short second antennal flagella can be seen on some specimens (Plate 5.8a).

Eight thoracic limbs can be seen on a 'ghost' specimen similar to the type 'B' preservation described by Briggs and Clarkson (1985a). The first thoracic limb is much shorter than the following seven and is interpreted as being the maxilliped. The seven posterior pereiopods are similar, biramous and decrease in length posteriorly after the fourth. All the pereiopods have multi-segmented distal ends.

The pleura of the second abdominal somite are large rounded and overlap those of the first and third. The pleura of the third through fifth somites are more pointed and point posteriorly. The sixth somite is approximately the same length as the telson but this can vary slightly from one population to another. There are paired right-angled grooves symmetrically placed along the dorsal mid-line of the abdomen of the second to fifth somites. The posterior dorsal

mid-line of the fifth abdominal tergite is drawn into a spine extending only a short distance over the sixth tergite. The pleopods are poorly preserved in most specimens, but when seen, are long with biramous blade-like articles.

The telson has a median sulcus dorsally producing two lateral tear-drop ridges each of which terminate in a short spine. The posterior margin of the telson is slightly concave with a row of shorter spines. The anus is ventral to the telson and is represented by a tubercle in a pore opening posteriorly (Plate 5.9f). The endopodal uropod extends as far as the telson, has a longitudinal groove, and robust setae along its inner margin. The blade-like exopodal uropod also has a medial groove, robust bifurcating setae, and is almost double the length of the endopod. The setae are similar in structure to those of the antennal scale. The uropodal exopod has diaeresis and terminates in a rectangular flap at the distal most end (Plate 5.9b,e,f).

Remarks.- *Palaemysis* has now been found at the same stratigraphic horizon at a number of localities near Glasgow. It is found associated with a number of other crustaceans in dark laminated shales. The associated eumalacostracans, such as *Crangopsis*, *Minicaris*, *Tealliocaris*, and *Tyrannophontes*, are not very different to the associated faunas at the other localities at Granton and Glencartholm.

The localities for *Palaemysis* are found at a variety of stratigraphic horizons, but show a remarkable continuity in the associated crustaceans, especially at the Lower Carboniferous localities (Granton, Glencartholm, and Bearsden). The Westphalian locality (Greengairs) lacks this diversity but may have been affected by preservational factors or environmental conditions.

Palaemysis was synonymised with *Anthracophausia* by Brooks (1969), and the specimens from Bearsden were identified as *Anthracophausia* by Wood (1982). There are, however, a number of differences between these two genera, with the result that *Palaemysis* is here resurrected as a separate genus from *Anthracophausia*. The differences include;

1) the rostrum of *Anthracophausia* is very distinct and falcate (Schram

1979) whereas *Palaemysis* has a very short spine-like rostrum (see Plate 5.7a);

2) the anterior spinose appendage has not been recorded in *Anthracophausia* prior to the discovery by Wood (1982), but a long second antenna can be clearly seen in some specimens (Schram 1979);

3) the telson of *Anthracophausia* is triangular and the same length as the uropodal exopods and in *Palaemysis* the telson is rectangular with two lateral oval ridges and is only two thirds as long as the uropodal exopods (see Fig. 5.21);

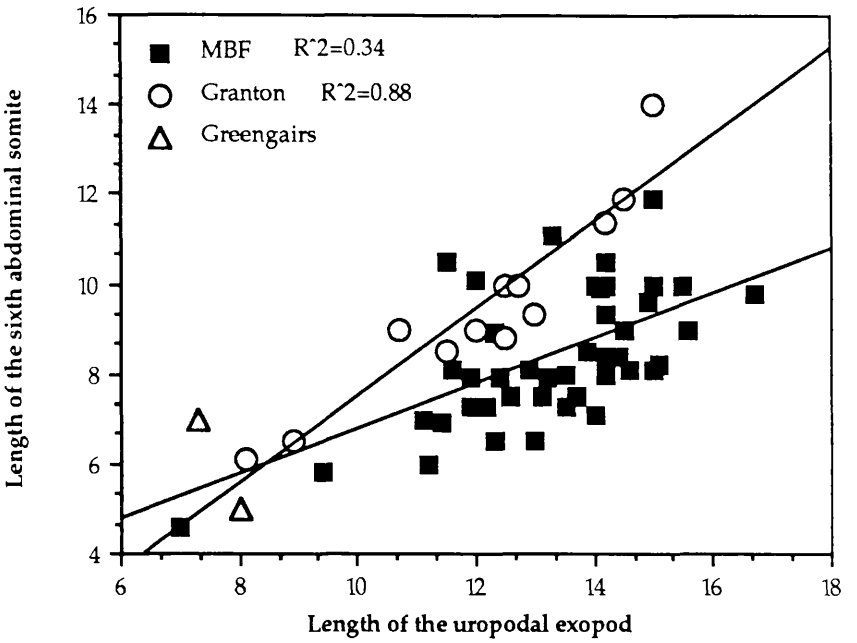
4) the shape of the uropodal exopod is blade-like with a straight inner and outer edge in *Palaemysis*, whereas in *Anthracophausia* the setae form a very rounded distal end (see Fig. 5.21);

5) the pleura on the abdomen are similar on all somites in *Anthracophausia*, whereas on *Palaemysis* the second abdominal pleura are enlarged to partially cover those of the first and third (see Fig. 5.19b).

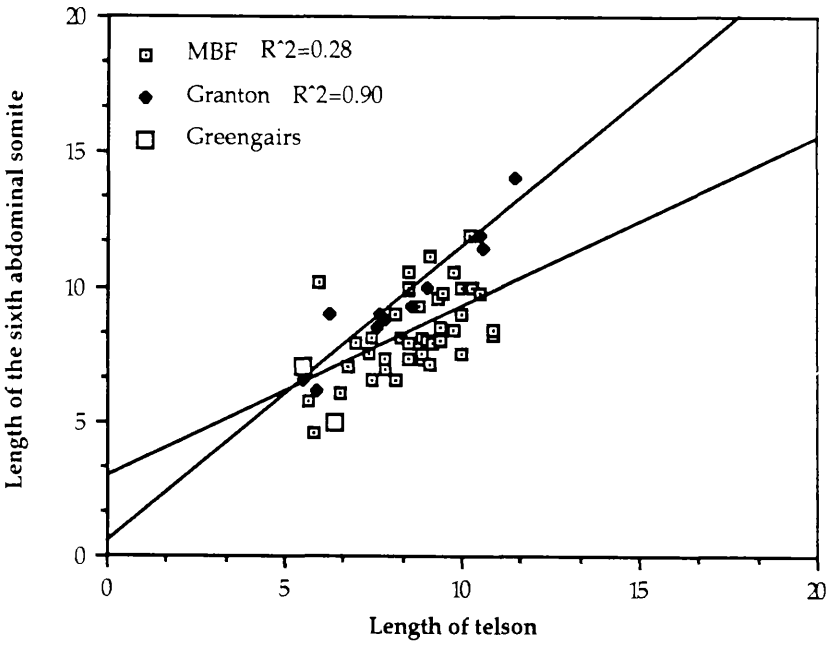
There are a few specimens of *Palaemysis*, although a lack of complete specimens, from localities other than Granton and Bearsden. No clear morphological differences could be observed other than those which could be related to preservational differences. For these reasons, only one species of *Palaemysis* has been resurrected. Peach (1908) recognised the different species on the basis of relative lengths of the various lengths of the tail fan and sixth abdominal somite. These factors are not considered enough to designate different species due to the spread of results obtained, and the small number of specimens involved. As there are more specimens available from Granton and Bearsden, a statistical test was performed on the relative lengths of the sixth abdominal somite, the uropodal exopod, and the telson to determine whether more than one species could be recognised.

Figure 5.17 Graphs showing the relative lengths of the telson (lt), the sixth abdominal somite (la6), and the length of the uropodal exopod (luex) of *Palaemysis* different localities (MBF=Manse Burn Formation). a) la6/luex; b) la6/lt; c) lt/luex. (measured in mm).

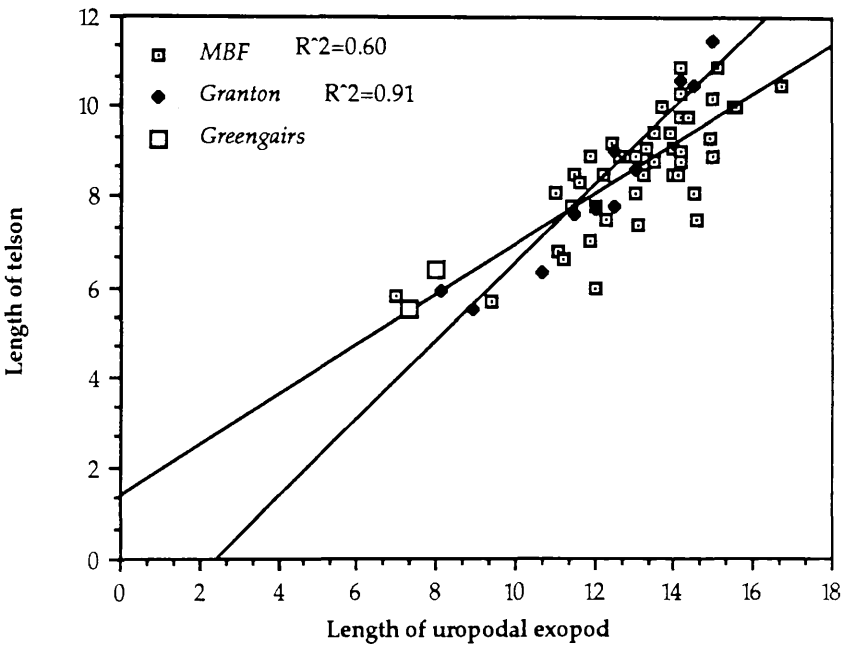
a)



b)



c)



The length of the sixth abdominal somite is relatively shorter in specimens

from the Shrimp Member (Bearsden). In the Manse Burn Formation, where the cuticle is well preserved, the fifth abdominal somite may slightly overlap that of the sixth. At Granton, most of the specimens are preserved as 'ghosts' permitting the full length of the sixth abdominal somite to be visible and hence may be seen to be slightly longer. The other alternative is that there is a real difference in the relative lengths of the sixth abdominal somite. However, while this differentiation may exist, single morphometric differences are not thought to be strong enough to designate new species, as bias can result from preservation or population size. Specimens of *Palaemysis* from Granton are, therefore, not regarded as a separate species from the specimens from the Shrimp Member.

The most noticeable structure of *Palaemysis* is the spinose frontal appendage previously described as a raptorial second antenna (Wood 1982). This appendage, however, is probably not the second antenna as a short flagellar appendage can be seen to emanate from the base of the antennal scale can be seen on the complete specimen figured by Wood (1982, fig. 4) and Schram (1986, fig. 9-3). The question still remains as to what this appendage could represent. It cannot be the first antenna, or any of the thoracic appendages as these are easily accounted for. The only limbs left which it could represent are the maxillae, the maxillules, or the mandibular palp. One extant crustacean holds a clue to the origin of this limb. *Petalophthalmous* W-Sühm 1875 has long spinose mandibular palps which extend well beyond the distal end of the antennal scale (Tattersall and Tattersall 1951, Tattersall 1968, Schram 1986). The palp of *Petalophthalmous* is not multiarticulate as the appendages are in *Palaemysis*. As all these limbs overlap and are fragmented at the proximal ends it is impossible from the present specimens to distinguish the true relationships between these appendages and the other frontal appendages. The illustration of *Palaemysis*, by Briggs and Clarkson (1983, pl. 20, fig. 4), appears to show that the antennal scale and the spinose appendage of *Palaemysis* have a common basal segment. There is, however, a segment between the antennal scale and the spinose appendage indicating that the spinose appendage is not the antennal flagellum.

The similarity between *Petalophthalmous* and *Palaemysis* extends further. The structure of the tail fan is also similar. In *Petalophthalmous caribbeanus* the telson is rectangular, and equal in length to the long sixth abdominal somite, and the distal end is armed with spines the longest of which occur on the distal lateral edges (Tattersall 1968). The uropodal exopod of *Palaemysis* is more like that of *Petalophthalmous armiger* although a lot shorter relative to the telson, in the way that the distal segment of the exopod is joined by a straight hinge. *Paralophogaster atlanticus* has a similar uropodal exopod with a straight hinge between the distal most article (Tattersall 1937). The shape of the telson is similar to that seen in *Mysidella americana* (Banner 1948). The flagellar nature of the distal articles of the pereiopodal endopods is common amongst the mysid crustaceans (Tattersall and Tattersall 1951). *Archaeomysis maculata* has a multi-segmented distal end to the third pereiopodal endopod, and in *Neomysis americana* and *Acanthomysis costata* the third through to the eighth pereiopodal endopods have multi-segmented distal ends. The abdominal pleura are rare in the mysids but have been recorded in *Gnathophausia ingens*. These pleura, however, are similar on all the abdominal somites, which differs from those of *Palaemysis* where the second abdominal pleura overlap those of the first and third.

Plate 5.7

a) Lectotype of *Anthracophausia dunsiana*, from Glencartholm, with arrow pointing to the large rostrum (BGS 5819; X4.6).

b) *Palaemysis dunlopi* from the Shrimp Member at Bearsden showing soft-part preservation. The arrow points to some blood vessels and muscle blocks (HM; X9.5).

c) *Palaemysis dunlopi* from Bearsden with arrow pointing to the second abdominal pleuron (HM A2751/1; X2.6). Photographed in toluene.

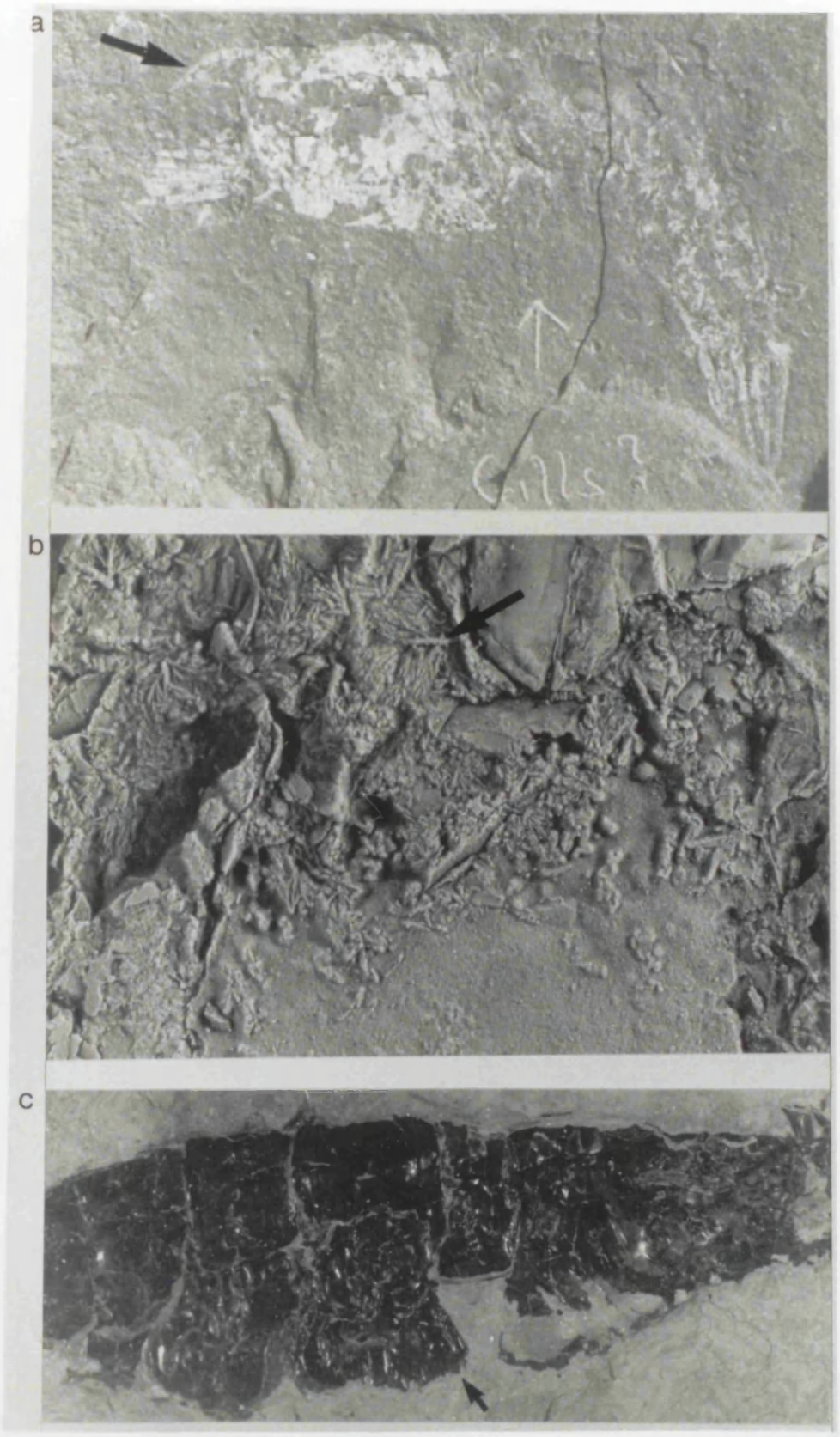

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Plate 5.8

a) Anterior appendages of *Palaemysis dunlopi* with arrow pointing to the second antenna (HM A2359; X3).

b) Anterior appendages of *Palaemysis dunlopi* photographed in water (HM A2745/3; X2.75).

c) Thoracic limbs (arrowed) of *Palaemysis dunlopi* photographed in water (HM G96; X2.75).

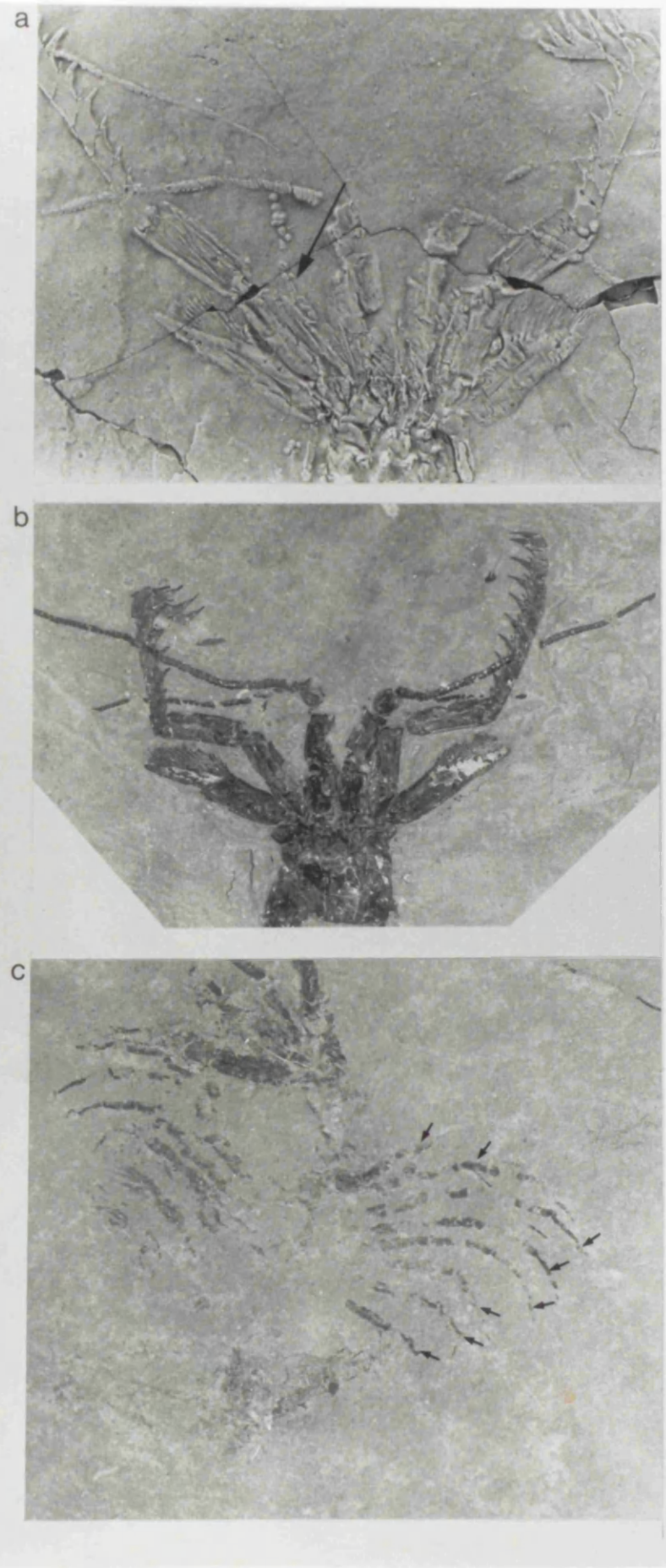
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Plate 5.9

a) Articulated specimen of *Palaemysis dunlopi* showing pleopods (arrowed) (HM A2740/1; X2.5).

b) Tail fan of *Palaemysis dunlopi* (HM A2745/6; X4).

c) Last four abdominal somites of *Palaemysis dunlopi* showing the abdominal grooves (small arrows) and the spine on the fifth tergite (large arrow) (HM A2747/3; X5).

d) Anterior of *Palaemysis dunlopi* showing mandibles (arrowed) (HM A2745/6; X6.25). Photographed in toluene.

e) Tail fan of *Palaemysis dunlopi* (HM A2749/4; X4).

f) Ventral view of tail fan of *Palaemysis dunlopi* showing anal pore (arrowed) (HM A2750; X2.1).

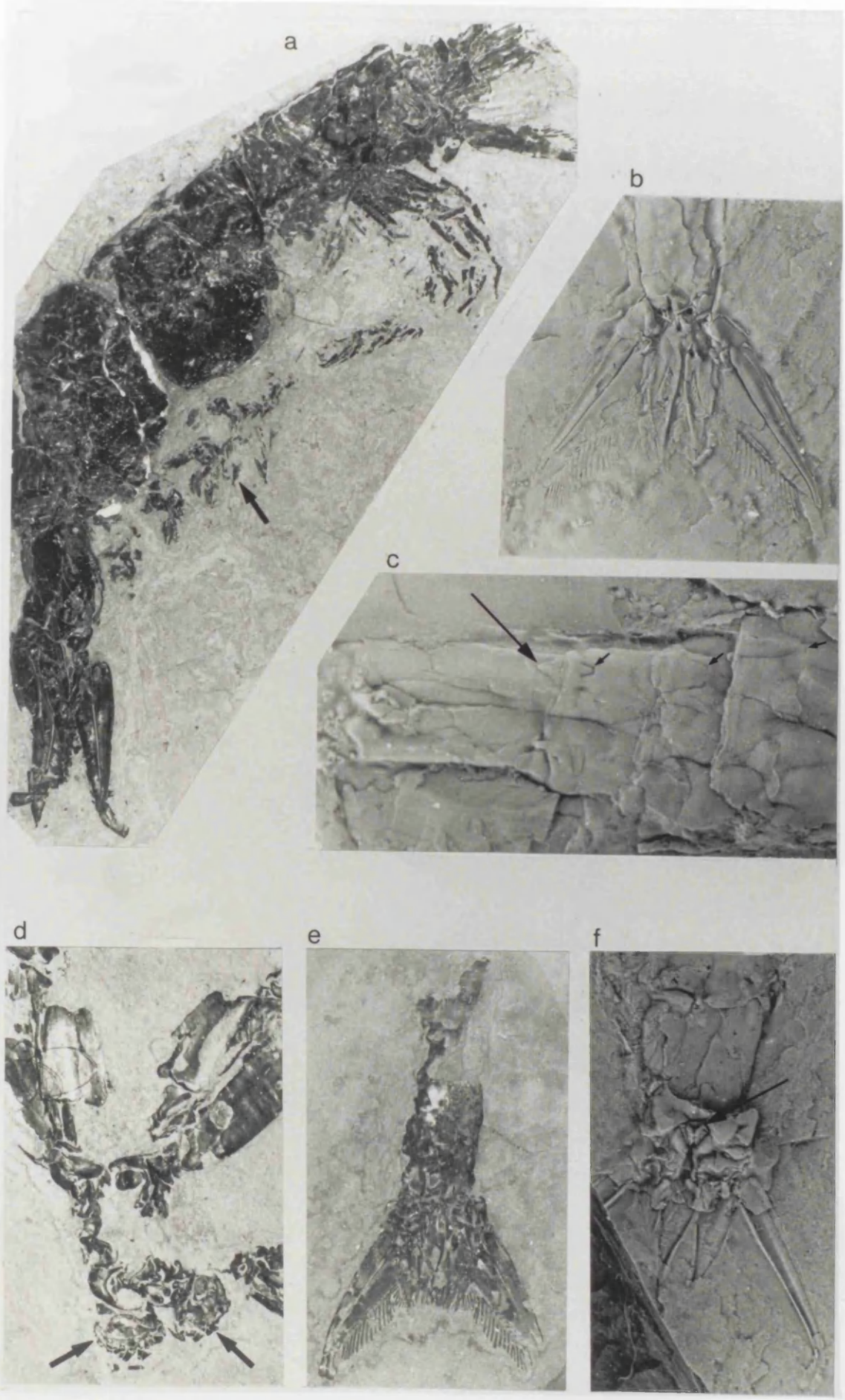
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Figure 5.18

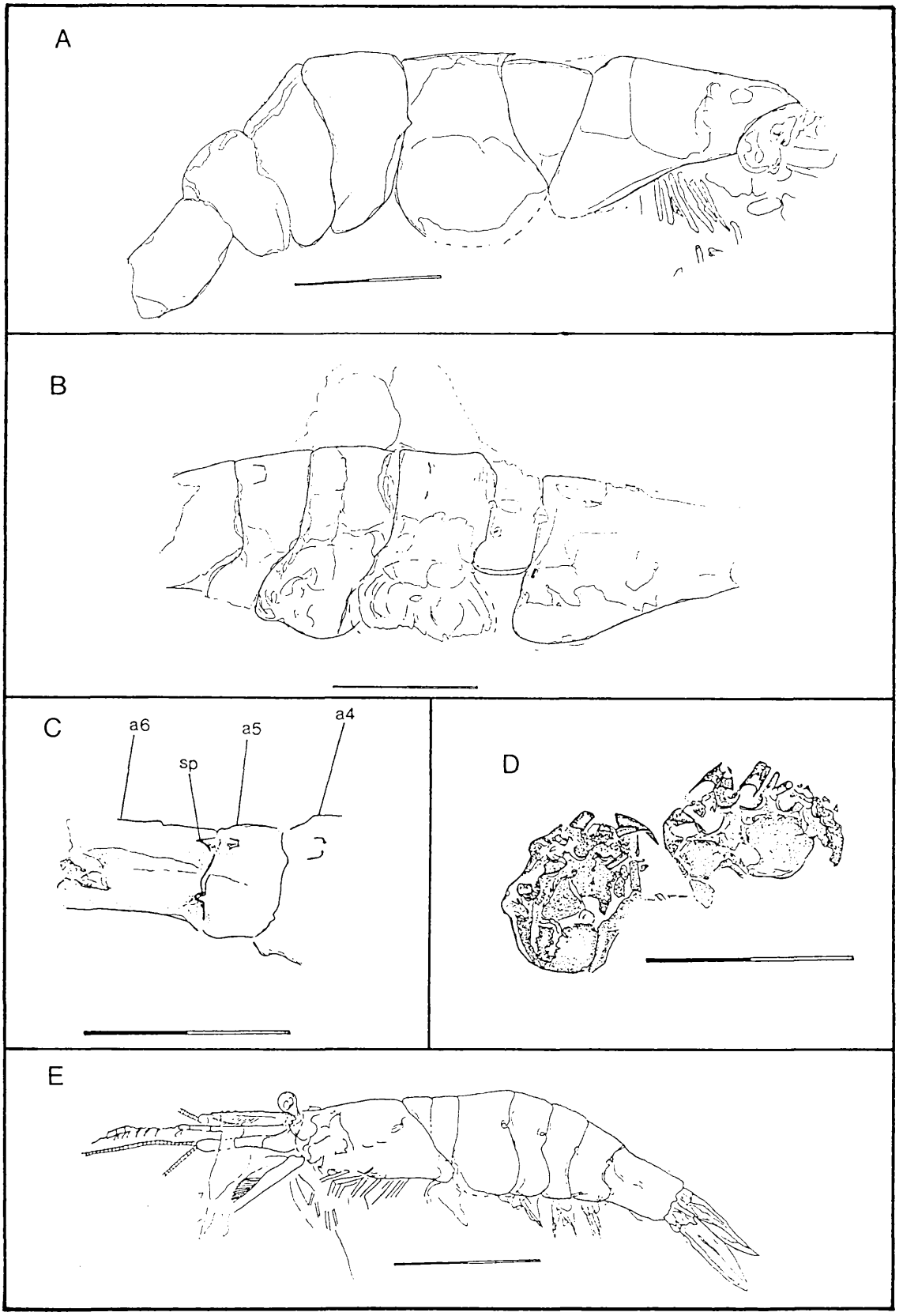
a) Outline of lateral body shape of *Palaemysis dunlopi* (HM A2740/1; scale-bar=0.5cm).

b) Dorsal view of the abdomen of *Palaemysis dunlopi* showing the grooves on the 2nd, 3rd and 4th abdominal tergites (HM A2751/1; scale-bar=0.5cm).

c) The 4th (a4), 5th (a5) and 6th (a6) abdominal tergites showing the abdominal grooves and the spine (sp) on the 5th abdominal tergite (HM A2747/3; scale-bar=0.5cm).

d) Mandibles of *Palaemysis dunlopi* (HM A2745/6; scale-bar=0.25cm).

e) Specimen of *Palaemysis sp.* from Granton (Grant Institute Edinburgh; scale-bar=0.5cm).


A
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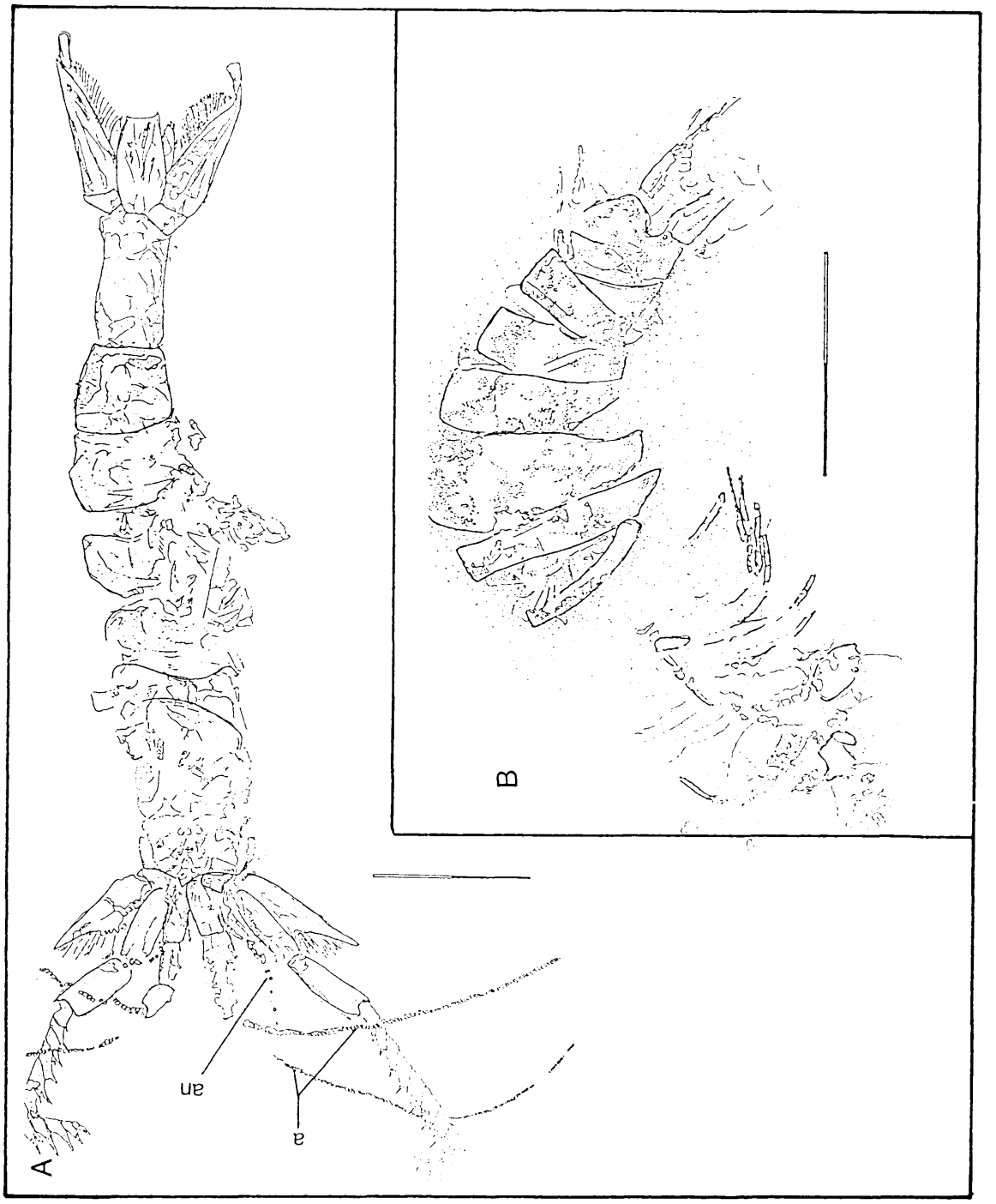

Figure 5.19

a) Articulated dorsal specimen of *Palaemysis dunlopi* showing the first (a) and second (an) antennae (HM A2359; scale-bar=1.0cm).

b) Specimen of *Anthracophausia dunsiana* from Glencartholm showing the form of the abdominal pleura (BM I.519; scale-bar=1.0cm).

Figure 5.20

a) Relationship between the spinose frontal appendages (sfa) and the mandibles (md) (HM A2745/6; scale-bar=1.0cm). an=first antennae

b) Anterior appendages of *Palaemysis dunlopi* (HM A2745/3; scale-bar=1.0cm). sfa=spinose frontal appendages, an=first antennae, as=antennal scale.

c) Detail of a thoracopod showing the multiarticulate distal end (HM A2745/6; scale-bar=0.5cm).

d) Eight thoracopods (th1, th8) of *Palaemysis dunlopi* (HM G96; scale-bar=1.0cm).

e) Thoracopods of a specimen of *Palaemysis sp.* from Granton showing similar multiarticulate distal ends (HM; scale-bar=1.0cm).

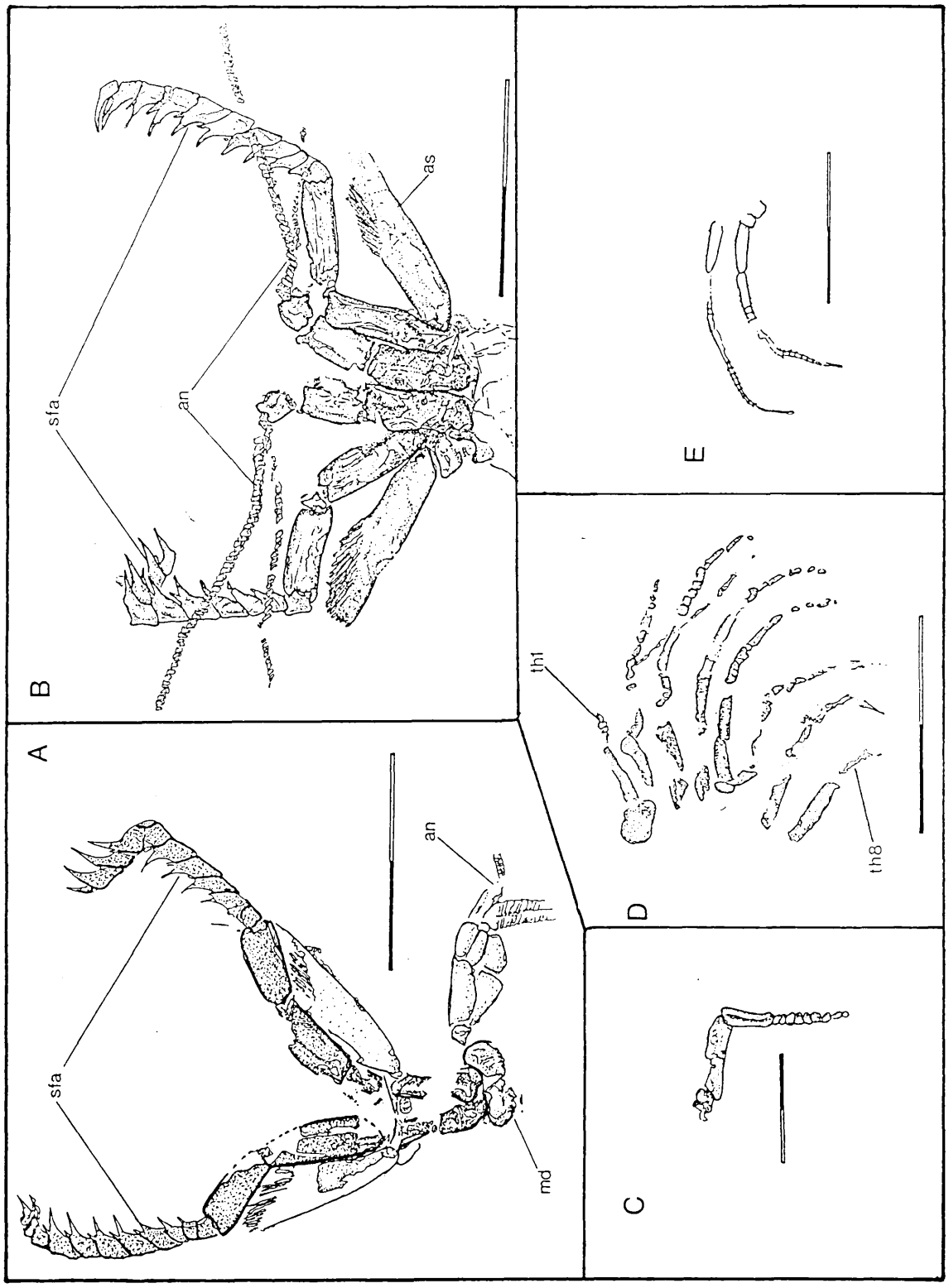

Figure 5.21

a-f) Tail fans of *Palaemysis dunlopi* a) HM A2745/6; scale-bar=1.0cm, b) HM A2751/4; scale-bar=1.0cm, c) lateral view of HM A2750/6; scale-bar=1.0cm, d) HM A2749/4; scale-bar=1.0cm, e) ventral view of HM A2750; scale-bar=1.0cm, f) specimen from Granton HM; scale-bar=1.0cm. te=telson, uen=uropodal endopod, uex=uropodal exopod.

g & h) Tail fans of *Anthracophausia dunsiana* for comparison (HM; scale-bar=1.0cm).

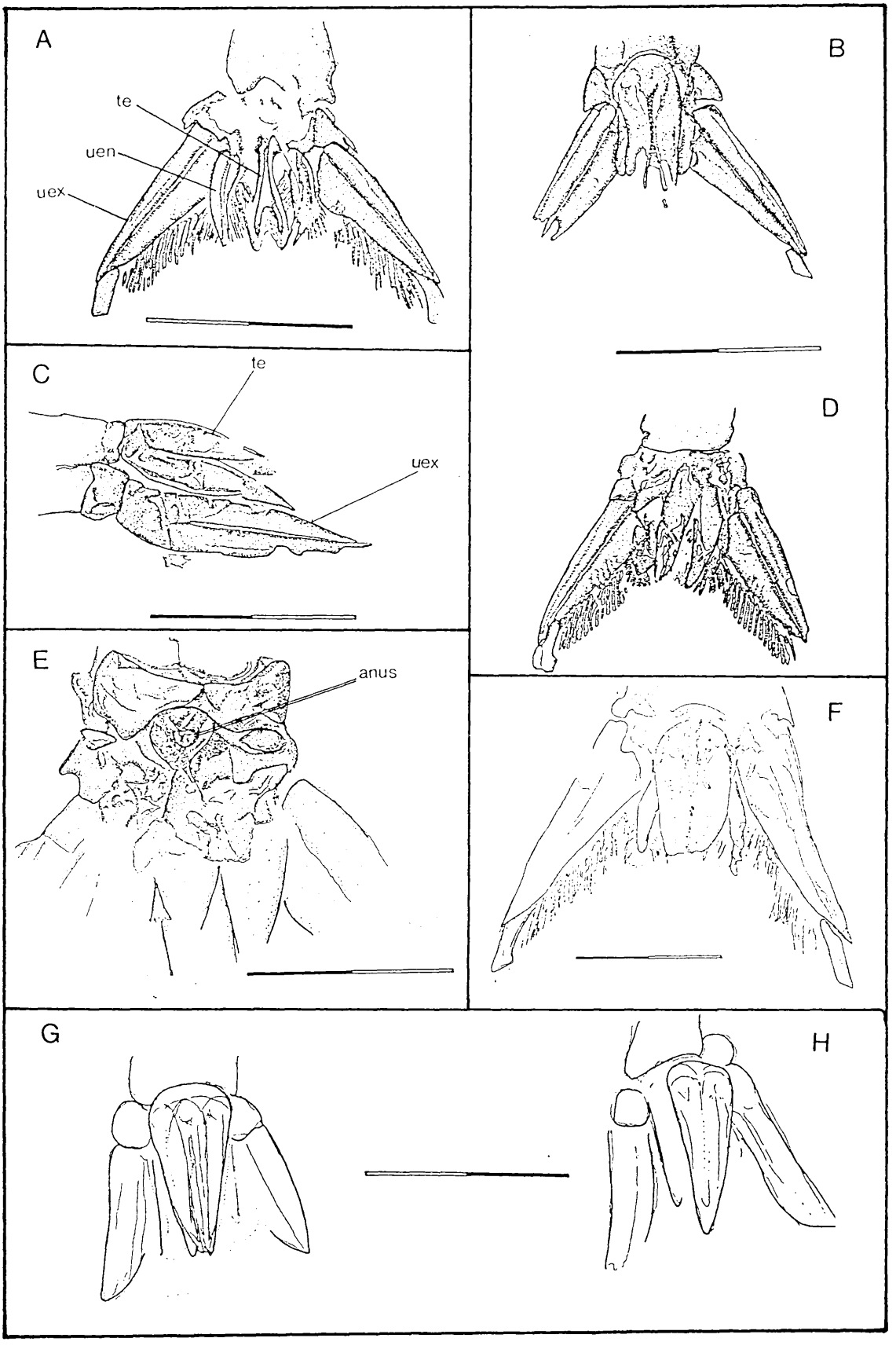
A
te
uen
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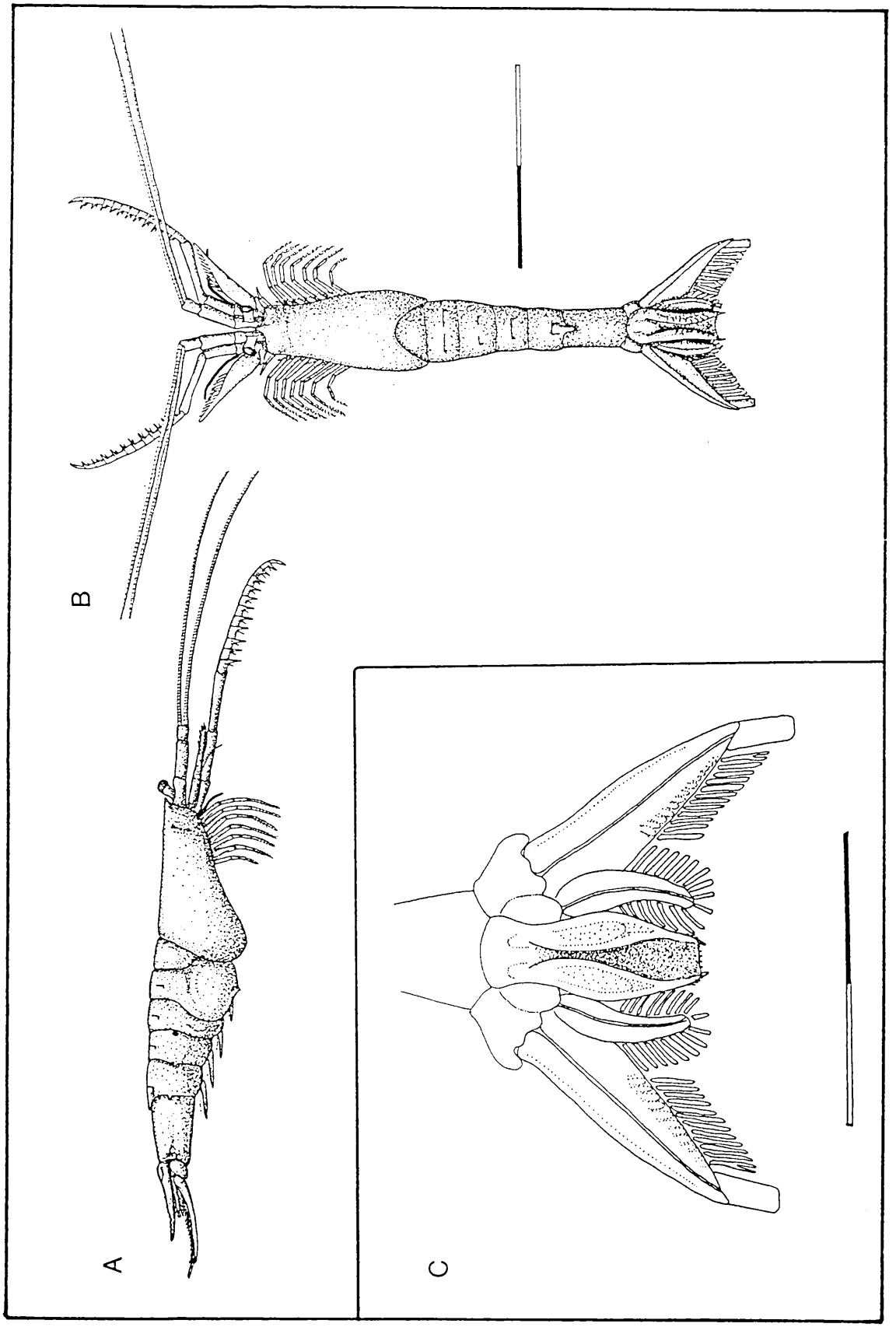
Figure 5.22

a & b) Lateral and dorsal reconstruction of *Palaemysis dunlopi* (scale-bar≈2.0cm).

c) Reconstruction of the tail fan of *Palaemysis dunlopi* (scale-bar≈0.5cm).



Order Palaeocaridacea Brooks 1962

Family Squillitidae

Genus *Minicaris* Schram 1979

Type species.- *Minicaris brandi* Schram 1979.

Diagnosis (Schram 1979, p109).-Peduncles of first and second antennae subequal. All thoracic segments equal in size. Uropods blade-like.

Minicaris brandi Schram 1979,

Plate 5.10a-g; Figs. 5.23a-e, 5.24.

1979 *Minicaris brandi* Schram. p109-112, figs. 52-53.

Holotype.-GSE 13056 from the Long Livingston Borehole no. 25, Lower Oil Shale Group (Fig. 5.23b).

Diagnosis.- As for genus.

Material.- Six specimens were obtained during the excavation of the Bearsden locality, and four more were recovered from the Red Cleugh Burn locality. All specimens are from the Shrimp Member, and from the base of the Nodular Shale Member (Wood 1982), of the Manse Burn Formation.

Description.- The three peduncles of the antennules extend as far as the anterior margin of the antennal scale. The antennal scale arises from the second peduncular segment of the second antenna. There are two segments distal to the position of the antennal scale which give rise to the antennal flagellum. The antennal flagella are at least as long as the thorax. The cephalon has a shield which extends anteriorly to a point.

The thoracic somites are all similar in length with two transverse grooves and lateral ridges or bosses on the tergites. The thoracic tergites are tuberculose, whereas, the sternites are smooth. The thoracopods are biramous with a

flagellar exopod and a stenopodous endopod. There may be some platey epipods although preservation is not good enough to be certain of this. Not all the thoracopods are well enough preserved, and a single stylized limb is represented on the reconstruction for this reason.

The first five abdominal somites are similar with posteriorly rounded pleura. The sixth segment is longer than the other five and is rectangular. On the fifth abdominal somite there is a small process on the lateral margin which may have originally been a small spine.

The pleopods, which are better preserved than the thoracopods, are biramous, annulate, and setose, with one ramus longer than the other. The telson is narrow with twelve long (≈200μm) lateral spines on each side. The posterior margin of the telson has an additional pair of spines seen only under high magnification (≈40μm). The uropods are approximately the same length as the telson and are blade-like with a median groove. The uropodal endopod is slightly smaller than the exopod which has rounded diaeresis.

Remarks.- Several features of *Minicaris*, described here, differ from the original description by Schram (1979). The telson does not appear to form a pleotelson with the sixth abdominal somite. No tergal preservation of the original specimens were reported by Schram (1979). The structures preserved on specimens from the Manse Burn Formation are reminiscent of *Squillites spinosus*, although, not enough detail is preserved of *Minicaris* to make it congeneric with *Squillites*. The similarities between these two genera include; the shape of the cephalic shield, the ornamentation of the thoracic tergites, the morphology of the thoracopods and the setiferous pleopods, the remnants of a spine on the fifth abdominal somite, and the morphology of the tail fan.

There are, however, a number of differences which would suggest, even if *Squillites* and *Minicaris* are congeneric, that they would not be considered as conspecific. The number of spines on the telson of *Squillites spinosus* (38) is greater than on the telson of *Minicaris brandi* (26), the sculpturing of the abdomen is greater in *Squillites* than in *Minicaris*, and the uropodal exopod of

Plate 5.10

a) Ventral view of the thorax of *Minicaris brandi* showing pereiopodal (thoracopodal) foramen (arrowed) (HM Min 1; X100).

b) Dorsal view of thorax (HM Min 1; X50).

c) Surface texture of the thoracic tergites (HM Min 1; X100).

d) Biramous and setose pleopods of *Minicaris brandi* (HM; X100).

e) Distal portion of the telson showing dissolution holes in the cuticle (HM; X250).

f & g) Tail fans of *Minicaris brandi* (f=HM G99, g=HM A21502/2; both X32.5).

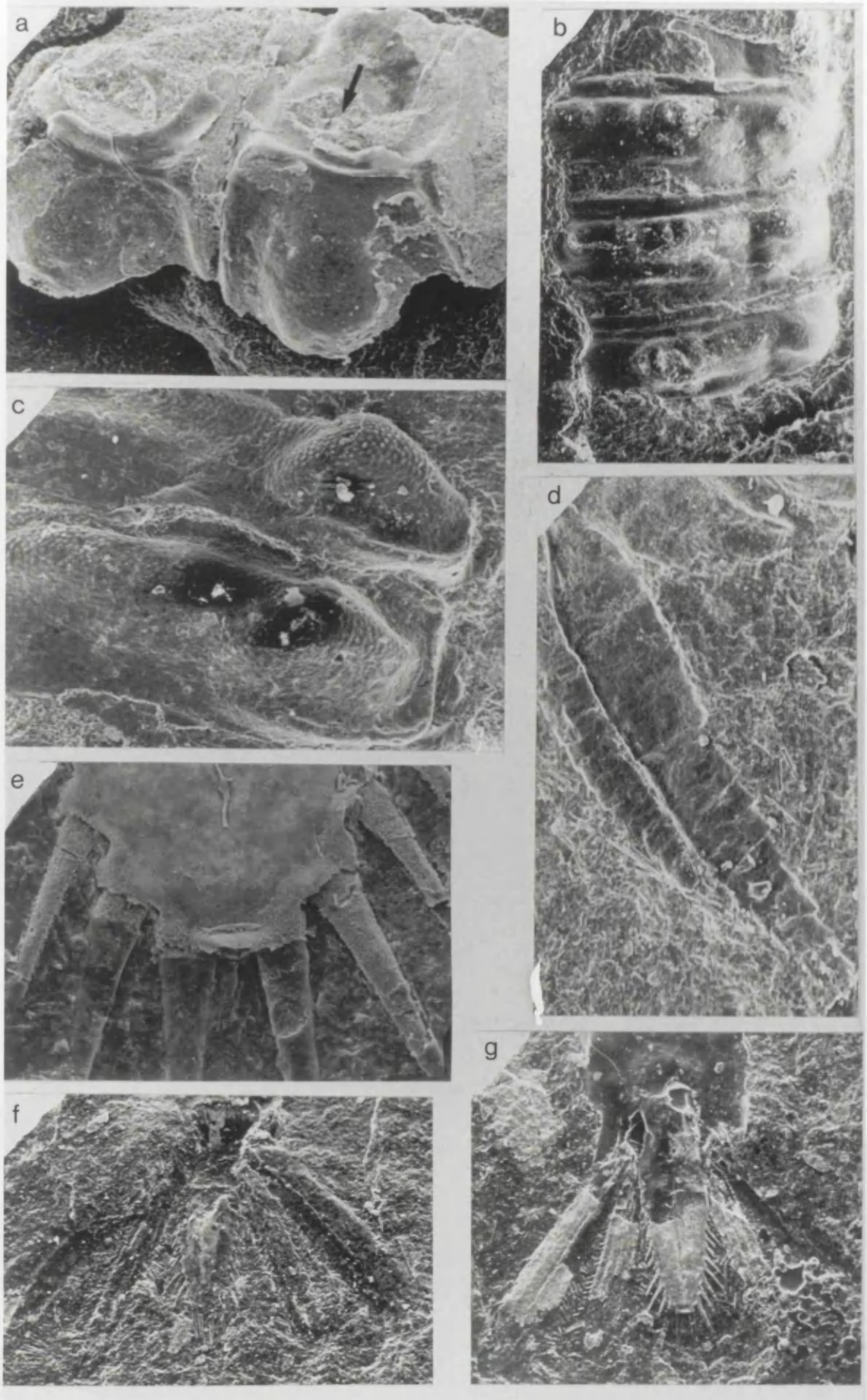

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Figure 5.23

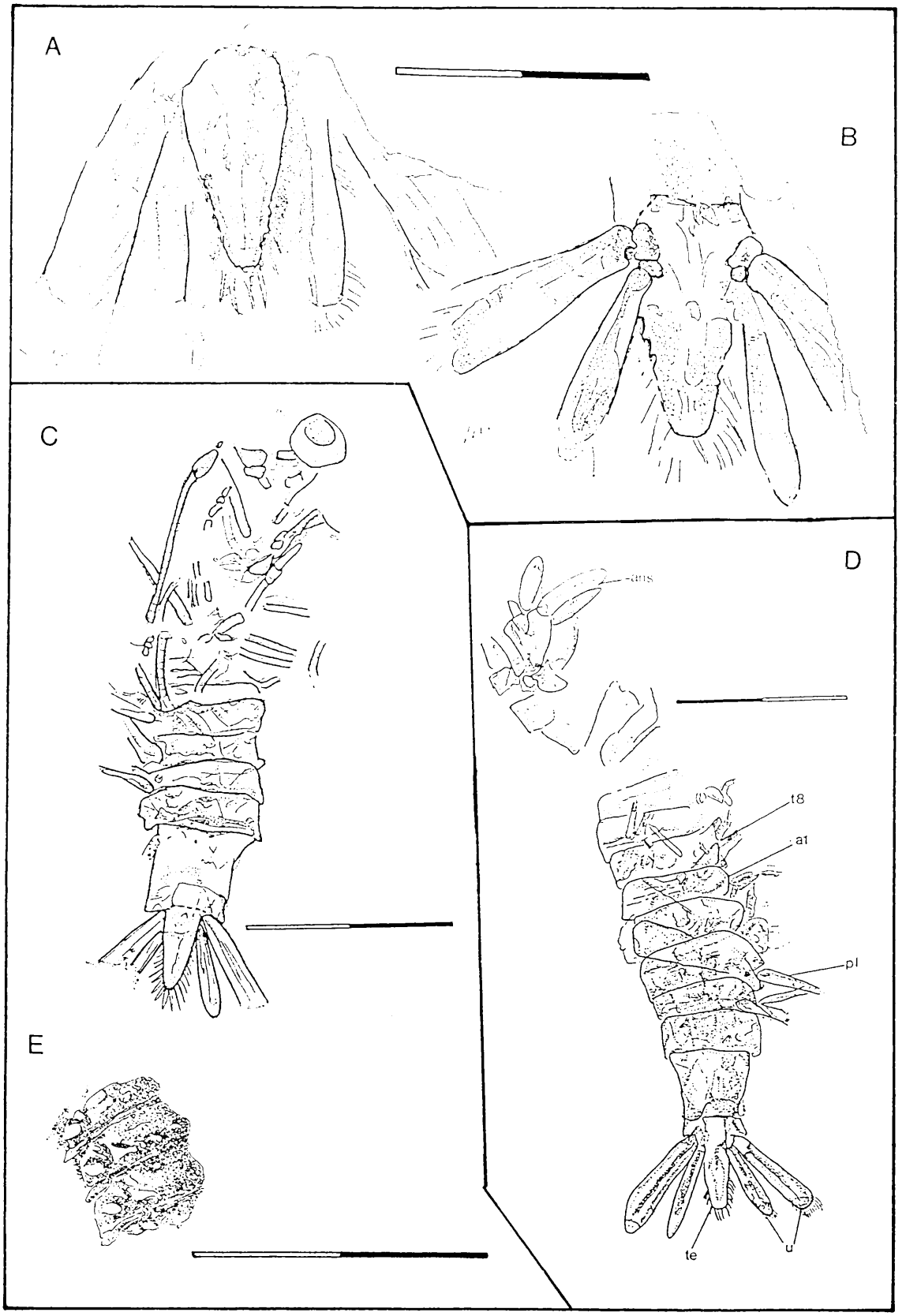
a) Tail fan of *Minicaris brandi* from the Nodular Shale Member, Bearsden (HM G99; scale-bar=0.1cm).

b) Tail fan of the holotype of *Minicaris brandi* (BGS 13056; scale-bar=as above).

c) *Minicaris brandi* from the Red Cleugh Burn locality (HM A21502/2; scale-bar=0.25cm).

d) *Minicaris brandi* from the Red Cleugh Burn locality (HM A21502/1a; Scale-bar=0.25cm). t8=eighth thoracic somite, a1=first abdominal somite, pl=pleopod.

e) Detail of the structure of the thoracic tergites (HM Min 1; scale-bar=0.1cm).


A
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t8
a1
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u

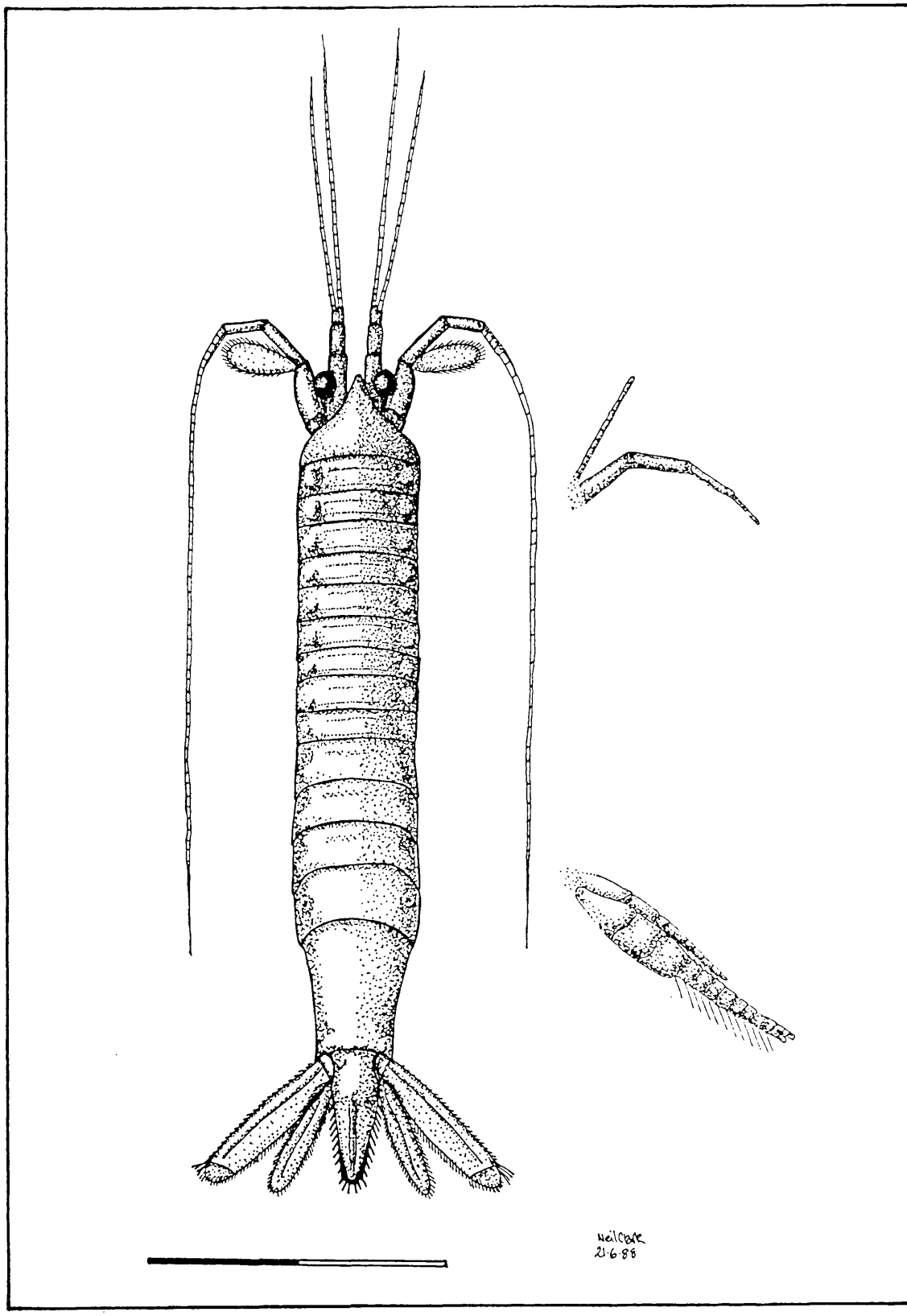

Figure 5.24
Reconstruction of *Minicaris brandi* showing structure of thoracopods and pleopods (scale-bar≈0.25cm).

Squillites has no diaeresis. *Minicaris* has also been found in the Viséan, Granton Shrimp Bed, near Edinburgh (Briggs *et al. in prep.*), where it occurs associated with crustacean genera similar to those found in the Shrimp Member of the Manse Burn Formation. The distribution of this genus appears to be restricted to the Midland Valley of Scotland and ranges from the Viséan into the Namurian.

Class Maxillipoda

Subclass Copepoda

Order Halicyna

Genus *Cyclus* De Koninck, 1841

Type species.- *Agnostus? radialis* Phillips, 1836, *Cyclus radialis* (Phillips, 1836) from the Carboniferous Limestone at Bolland, Yorkshire.

Diagnosis (emended from Hopwood 1925. p305-306).- Carapace oval to subcircular, with posterior median ridge which may bifurcate anteriorly, radial structure to thoracic tergites.

Cyclus rankini Woodward 1868,

Plate 5.11a-c, 5.12a-g; Figs. 5.25a, b, 5.26a-c, 5.27a-d, 5.28a, b, 5.29a, b.

Diagnosis.- Subchelate anterior limbs, spines on thoracic limbs, and sixth thoracic limb modified to point antero-medially. Telson triangular with lobate and spinose furcae.

Description.- *Cyclus* is circular to oval in plan view with a dorsal shield (carapace) which extends to cover the whole animal. The limbs, antennae, and caudal furcae extend beyond the edges of the carapace. The carapace is composed of two thin cuticular divisions of which the outermost or epicuticle is very thin and has been removed from most specimens to expose the slightly thicker lower division or exocuticle. The epicuticle has fine thread-like ridges with small pits covering the exterior surface. The exocuticle has a number of larger pores that cover the surface interpreted as cuticular ducts.

The carapace tapers posteriorly and is indented to expose the short telson and caudal rami. The anterior has bosses, is truncated and raised with a median ridge which narrows posteriorly where it splays into the outer margin. The limb bases are expressed on the dorsal surface of the carapace as a circular impression with radial sectors. The carapace extends beyond the limb bases to a marginal flange.

Two pairs of antennular flagellae, one longer than the body length with up to 60 articles, and the other shorter and seen only on one specimen. On one specimen (see Plate 5.12c; Fig. 5.28a) a short pair of anterior limbs are observed that may represent palps for manipulating food fragments in front of the mouth parts. Posterior to this are two pairs of similar, robust, sub-chelate limbs with the third to last article inflated and denticulate, and the terminal articles curved anteriorly over the inflated one. These are similar in character to the limbs of some parasitic copepods. The next five pairs of thoracic appendages are similar, seven-segmented, robust, have bristles on the lateral margins, and all curve anteriorly. The last appendage before the tail fan is slender, curved medially, and is interpreted as a sexual appendage or petasma. The radial limb bases are all laterally attached to each other and medially attached to the sternum.

The triangular telson and lobate caudal furca appears attached to the posterior end of the medial ridge of the thorax with either a much reduced or absent abdomen. The ellipsoid furcal lobes are laterally spinose.

Remarks.- The distribution of *Cyclus* in both coral reefs and laminated shales, suggests that it was mobile. However, the limbs and general morphology of the animal indicate that this was not so. *Cyclus* does not have the limb structure nor the body shape of a planktonic swimming copepod or a modified parasitic copepod. The distribution of *Cyclus* into different environments suggests, also, that it was not a benthic animal. The association of *Cyclus* with epifaunal bivalves, *Leiopteria*, attached to the cuticle suggests that it, also, lived epifaunally. The bivalve *Leiopteria* is found abundantly in pockets, possibly

representing epifaunal attachment to marine algae. The wide range of environments in which *Cyclus* can be found, therefore, indicates that it was transported into the different environments, possibly by floating marine algae also. Extant copepods commonly colonise the marine flora (Cummings and Ruber 1987, Bell *et al.* 1988).

The Copepoda are found in nearly all aqueous environments (Palmer, 1969, R200). The Calanoida include free swimming planktonic copepods, and the Cyclopoida include planktonic, benthic, and parasitic forms. Both these orders have superficial morphological similarities to *Cyclus*.

In *Cyclus* the prosome is much broader than the urosome and the antennules are long, similar to the Recent order Calanoida Sars, 1903, and to the Miocene to Recent order Cyclopoida Sars, 1903. The prosome, of *Cyclus*, consists of a head region covered dorsally and laterally by a cephalic carapace, a thorax with four to five segments bearing biramous appendages. The urosome consists of one or two thoracic somites with appendages, four to six abdominal appendages, and a terminal pair of setose caudal rami.

Plate 5.11

a) Ventral view of *Cyclus rankini* from the Shrimp Member at Bearsden (HM A2808b; X5). Arrow is pointing to the 'sexual' appendage.

b) Specimen from Lochermill associated with coprolite (HM ; X3.75)

c) Specimen from the Red Cleugh Burn locality showing the proximal articles of the thoracic appendages (HM A21498a; X13).

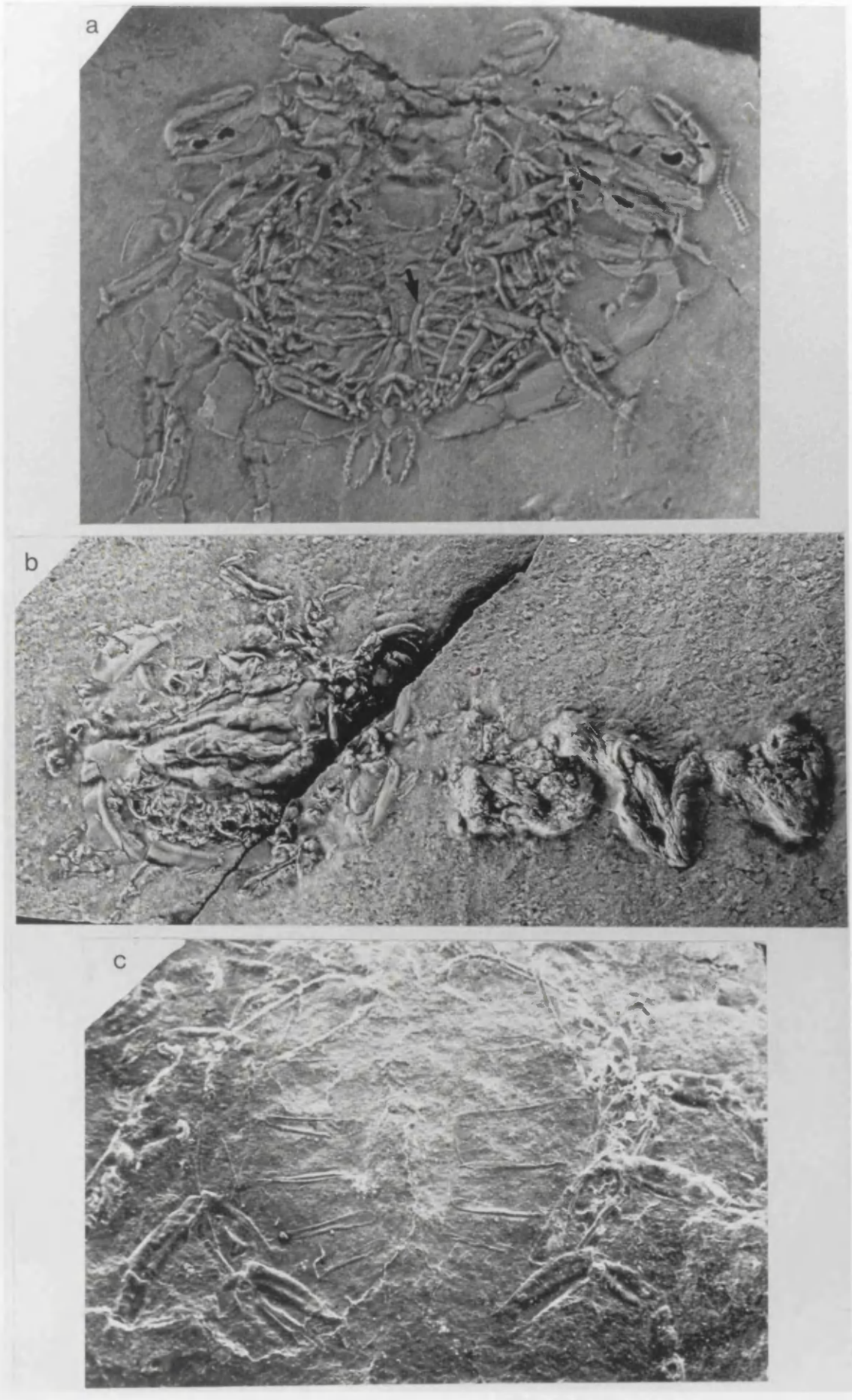
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Plate 5.12

a) Articulated specimen of *Cyclus rankini* from Bearsden with *Leiopteria* attached (arrowed) (HM; X4). Photographed in toluene.

b) Specimen of *Cyclus rankini* with the cephalic shield removed to show dorsal view of thoracic tergites (HM; X3.5). Photographed in water.

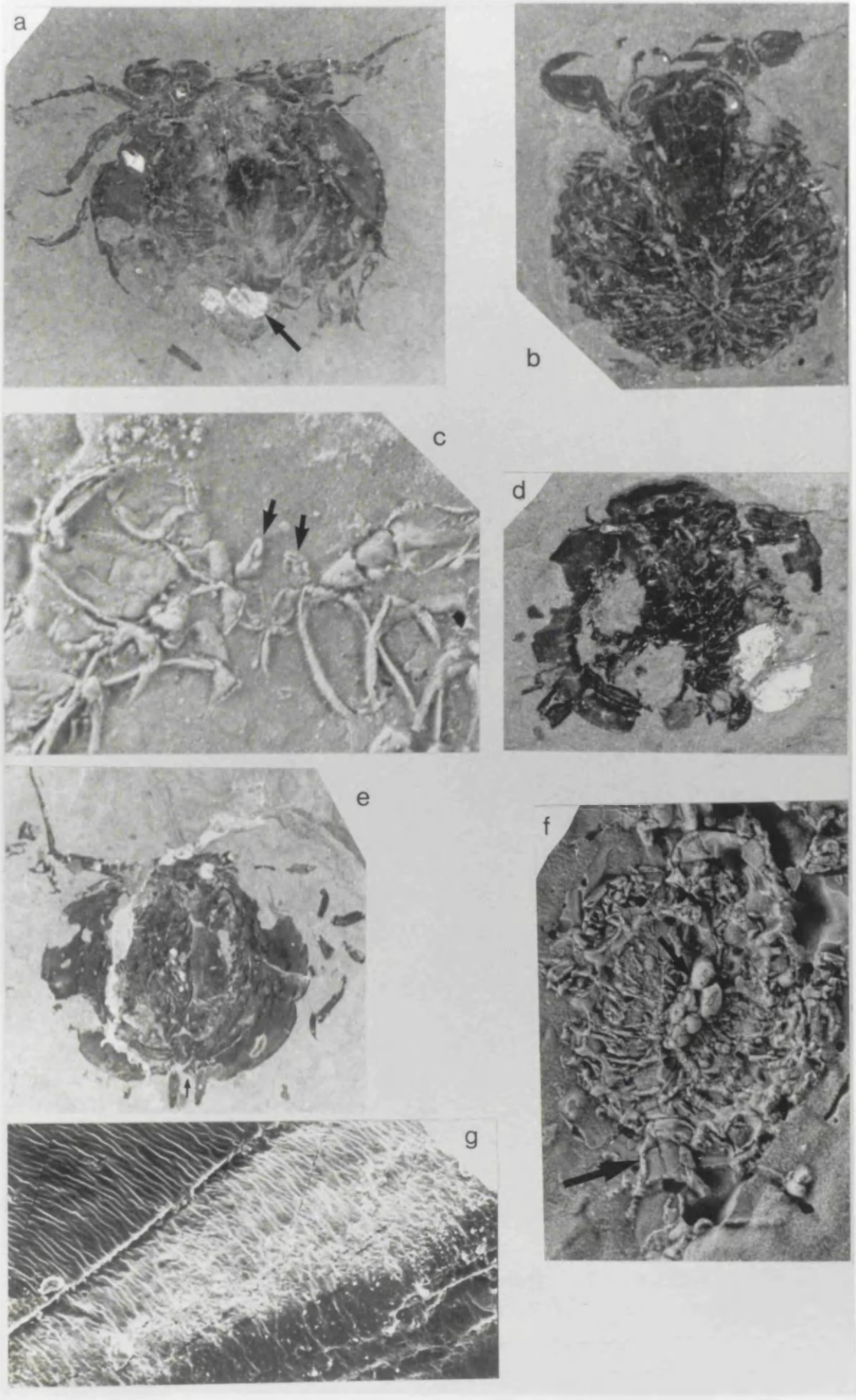
c) Anterior portion of *Cyclus rankini* showing small appendages which may represent mandibular palps (arrowed) (HM A2806/1; X15).

d) *Cyclus rankini* with *Leiopteria* (white) attached to the cephalic shield (HM; X7). Photographed in water.

e) *Cyclus rankini* showing the posterior margin of the cephalic shield curved anteriorly (arrowed) exposing the tail fan (HM; X4). Photographed in water.

f) *Cyclus rankini* prepared to show abdomen (large arrow) and ?gut (smaller arrow) (HM; X8.25).

g) Surface structure of the cuticle of *Cyclus rankini* (HM; X220).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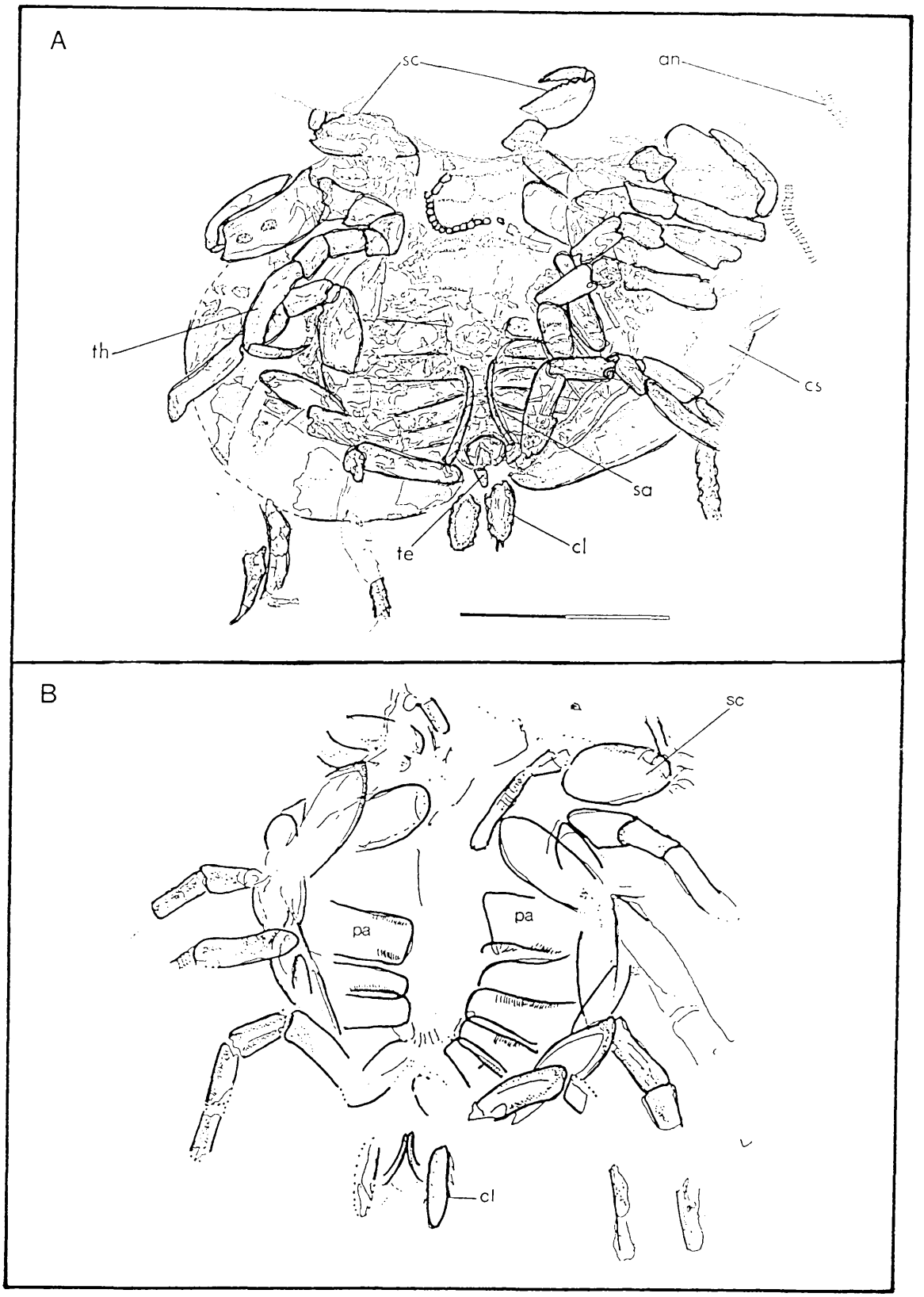

Figure 5.25

a) Ventral view of *Cyclus rankini* from Bearsden (HM A2808b; scale-bar=0.5cm). sc=subchelate anterior limbs, an=antenna, th=thoracopod, cs=cephalic shield, sa=?sexual appendage, te=telson, cl=caudal lobe.

b) Ventral view of *Cyclus rankini* from the Red Cleugh Burn (HM A21498a; scale-bar=as above). sc=subchelate anterior limbs, pa=proximal articles of the thoracopods, cl=caudal lobe.

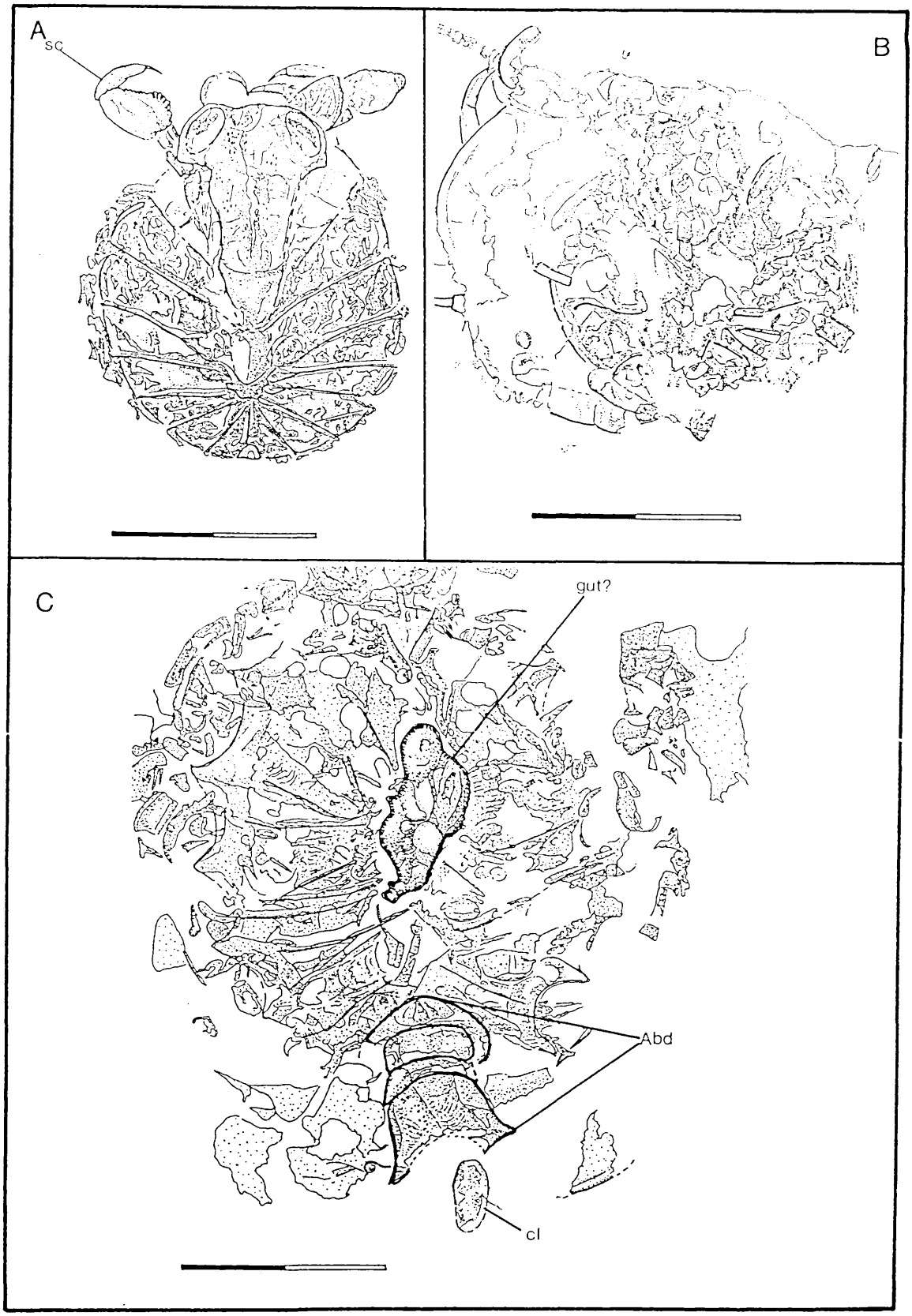

Figure 5.26

a) Dorsal view of *Cyclus rankini* with the cephalic shield removed to show the thoracic tergites (HM; scale-bar=0.5cm). sc=subchelate anterior limb.

b) Poorly preserved specimen of *Cyclus rankini* (RMS 1981.63.9b; scale-bar=0.5cm).

c) Ventrally prepared specimen showing abdomen (Abd) and possible gut preserved (HM, scale-bar=0.5cm). cl=caudal lobe.

Figure 5.27

a) Specimen of *Cyclus rankini* showing thoracic and cephalic appendages (HM A2806/1; scale-bar=0.5cm). sc=subchelate anterior limbs, th=thoracopods.

b) *Cyclus rankini* with *Leiopteria* (le) attached to the cephalic shield (HM; scale-bar as above). sc=subchelate anterior limbs, an=antenna.

c) Detail of the third thoracopod (HM A2807b; scale-bar=0.25cm). spb=spine base.

d) Specimen of *Cyclus rankini* from Lochermill associated with a coprolite (HM; scale-bar=0.5cm). sc=subchelate anterior limb, cop=coprolite.

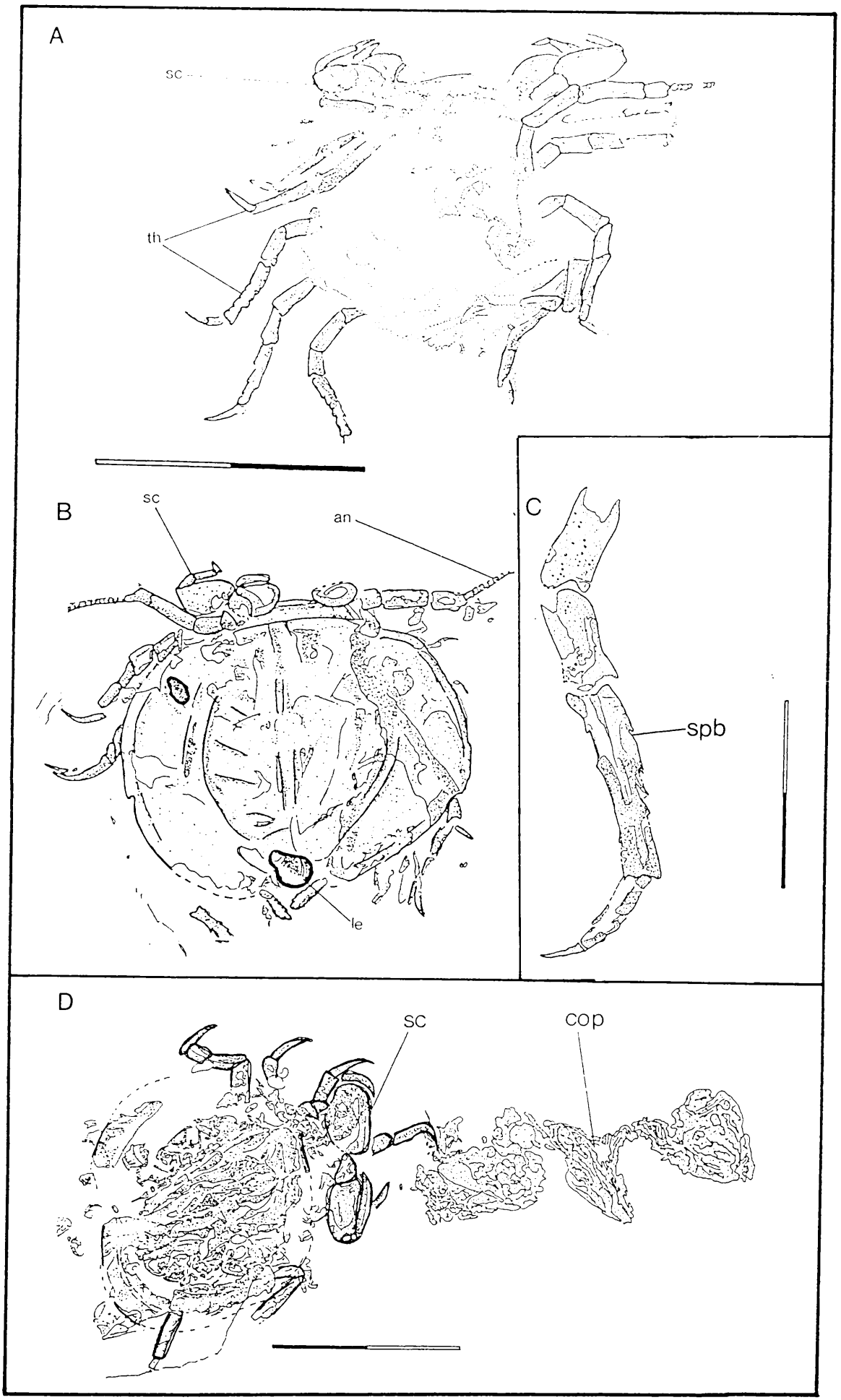
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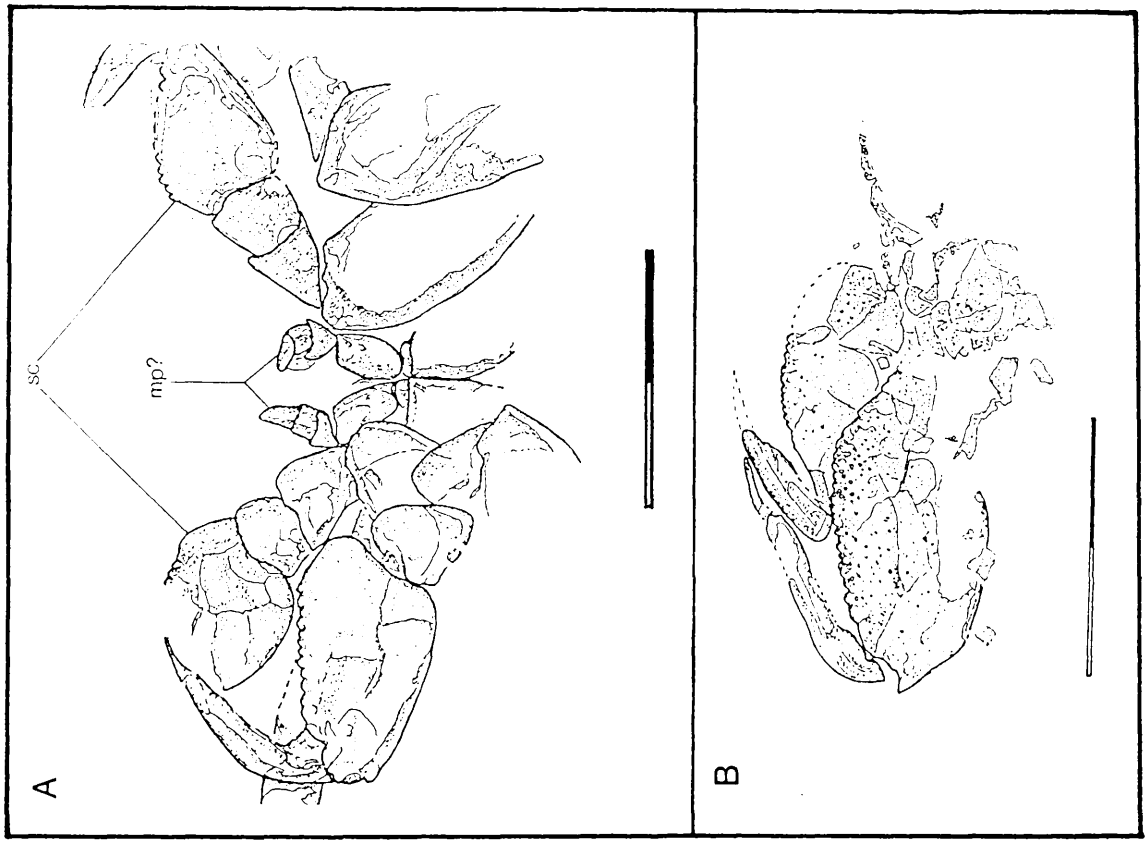
Figure 5.28

a) Detail of anterior limbs of *Cyclus rankini* (HM A2806/1; scale-bar=0.25cm). sc=subchelate anterior limbs, mp?=possible mandibular palp.

b) Detail of the subchelate anterior limbs (HM A2807b; scale-bar=0.25cm).



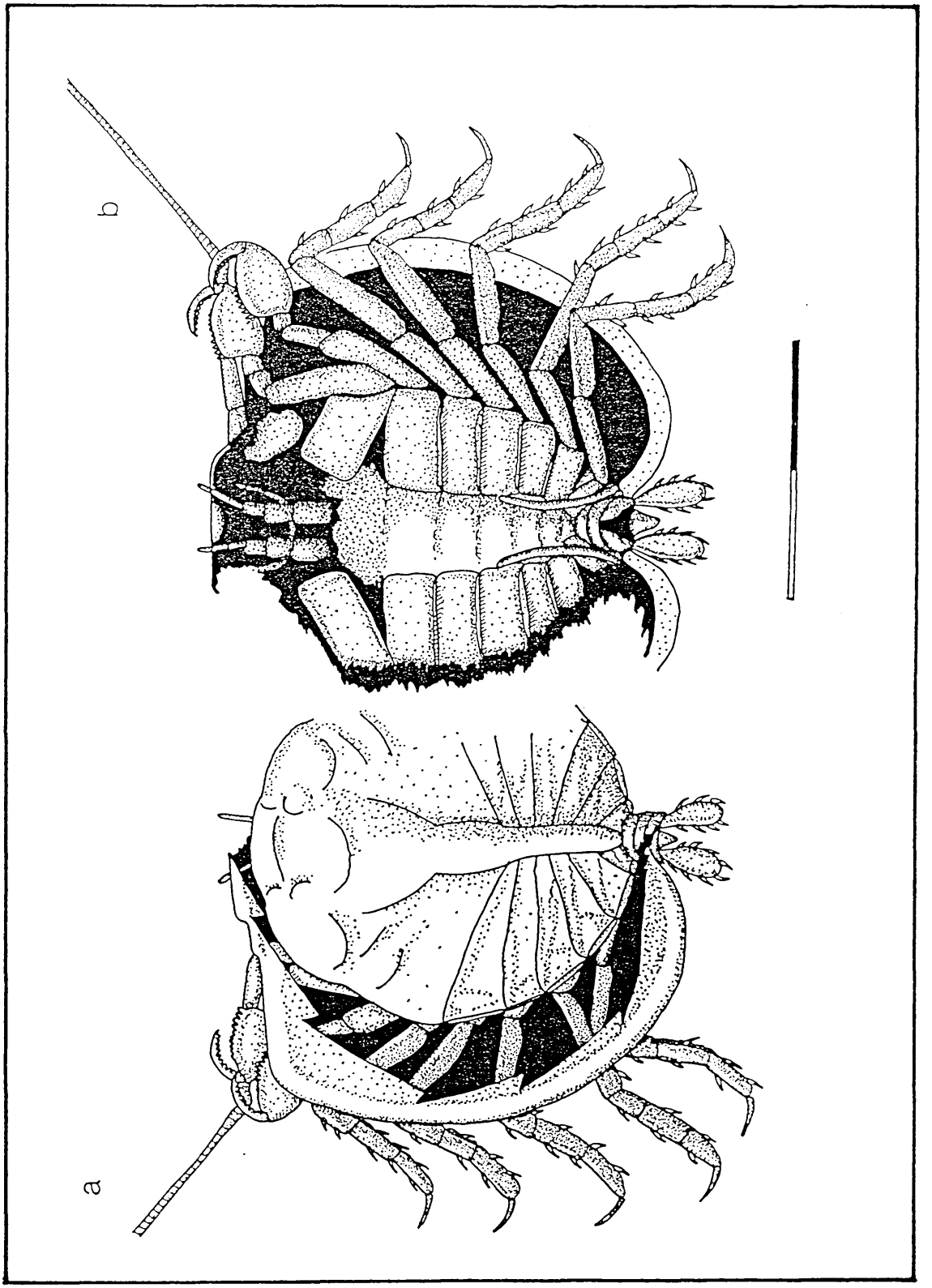


Figure 5.29

a) Dorsal reconstruction of *Cyclus rankini* with part of the cephalic shield removed to show the thoracic tergites.

b) Ventral reconstruction of *Cyclus rankini.*

(Scale-bar≈0.5cm)

5.6 **Cuticular microstructure** (Plate 5.13, 5.14).

Despite the volume of work done on fossil Carboniferous crustaceans, very little attention has been given to the cuticular micro-structures. Cuticular micro-structures have been described previously from some fossil crustaceans from the Silurian (Rolfe, 1962) and also from the Jurassic and Cretaceous (Neville and Berg, 1971, Taylor, 1973, Simpson and Middleton, 1985, Feldmann and Tschudy 1987). It is found that the cuticles of these crustaceans preserve much detail of the micro-structure as a result of varying degrees of diagenetic phosphatisation or decalcification. The cuticle of the Jurassic and Cretaceous decapods exhibit few differences to that of extant decapods, although Taylor (1973) noted the absence of tegumental ducts and the abrupt termination of the pore canals beneath the exocuticle of Cretaceous decapods.

Many of the structures observed here were previously thought to be features of extant crustaceans (Taylor 1973, p. 98). The pore canals terminating beneath the exocuticle of *Hoploparia stokesi* were thought to indicate a primitive condition, although they may have been obscured by diagenesis (Taylor 1973, p.99). The smaller pits on the exocuticle of *Tealliocaris* illustrated by Briggs and Clarkson (1985a, p.190 fig.15g; p.196 fig.21c-e) have been interpreted here as pore canals, and the larger pits as cuticular ducts. The polygonal structures on the epicuticle of the carapace and the epicuticle of the sixth thoracic endopod of *Tealliocaris*, illustrated by Briggs and Clarkson (1985a, p.176 fig.3h; p.197 fig.22c), indicate a uniform expansion of the epicuticle as the exocuticle and endocuticle harden after ecdysis

Three major subdivisions of the cuticle are recognised, the epicuticle, the exocuticle, and the endocuticle. The emergence line, where the ecdysial membrane forms during the absorption of the endocuticle (Travis 1954, 1955, 1957), can also be recognised at high magnifications on broken sections of the cuticle. The exocuticle usually has smaller laminar spacing than the outer

endocuticle in extant Crustacea, and the presence or absence of the latter can be used to differentiate between carcasses or exuviae in fossil specimens.

Etched and oblique sections of the cuticle of *Tealliocaris* seem to support the helicoid ultrastructural model of the cuticle by Bouligand (1965) (see Plate 5.13, 5.14). The pore canals form parabolic arcs in both oblique and etched surfaces similar to those seen in Cretaceous crustaceans (Dalingwater 1977) and extant arthropods (Neville 1975).

As the extent of calcification of crustaceans depends on which parts are more advantageous (Mills *et al.* 1976), the thicker cuticle of *Tealliocaris* (≈60μm) suggests that it needed to protect itself against environmental factors such as excessive diffusion of salts, or predators, more than did the crustaceans with thinner cuticles, such as *Palaemysis* (≈35μm) and *Crangopsis* (≈20μm).

The body of crustaceans has many sites for chemo- and mechano-reception (Phillips *et al.* 1980). They are positioned over most of the cuticle so as to respond to water currents or other stimuli. The tegumental ducts in the cuticle of *Tealliocaris* continue through the epicuticle to open as microscopic pores which may have originally been used for chemo- or mechano-reception. Briggs and Clarkson (1985a, p195) recorded closely spaced domes superimposed on fibres exhibiting a crescent distribution on the internal surface of the abdominal tergite of *Tealliocaris woodwardi* Peach 1908 from Gullane. The 'domes' are in fact large pits (>20μ diameter), representing the cuticular ducts, which are widely distributed within the exocuticle of the entire shrimp. The pores on the surface of the epicuticle of *Tealliocaris* are comparable in size (≈1μ) to the external expression of the pore canals of extant crustaceans (Neville 1975, p35). The fibres described by Briggs and Clarkson (1985a) in *T.woodwardi* from Gullane, are similar to the pore canals of extant crustaceans which are thought to be involved in the transport of wax or lipids to give some cuticular stability following ecdysis (Neville 1975, p. 35).

The concentration of tegumental ducts in the cuticle of *Tealliocaris* varies between localities where the salinity is thought to be marine, and those where

extreme salinities exist. At Gullane the number of tegumental ducts per sq. mm, depending on the carapace length, is greater than that found for the cuticle of *Tealliocaris* from Bearsden, Glencartholm, and Duns (Berwickshire) (Appendix 49d). The number of tegumental ducts per sq. mm decreases with increasing carapace length suggesting that the total number of ducts does not increase significantly with size. At Gullane, where the salinity conditions are non-marine, the number of tegumental ducts per sq. mm on the surface of the carapace is greater, indicating that it had to be more aware of the surrounding environment. If this is the case, then it is likely that the tegumental ducts were mostly used as sites for chemoreception, perhaps to monitor the salinity conditions.

Other structures such as the number of anterolateral spines on the carapace and on the antennal scale of *Tealliocaris* also vary between environments with different salinity conditions. At Gullane, and other localities with a low crustacean diversity, there are fewer spines on the antennal scales and on the carapace than at localities where there is greater crustacean diversity, such as Glencartholm and Bearsden.

The surface texture of *Palaemysis* is different to that of *Tealliocaris* in that it appears to lack the abundant pore canals and cuticular ducts on the exocuticle of the latter. *Crangopsis* and *Cyclus*, however, both have pitted epicuticles which may represent terminations of cuticular ducts. *Crangopsis* has a large number of tegumental ducts per sq. mm (≈1000 on the carapace) which may also reflect a need to monitor the surrounding salinity conditions, whereas, there are very few tegumental ducts visible on the surface of the cuticle of *Palaemysis*. The number of ducts in the carapace of *Crangopsis* per sq. mm is lower than that recorded for the Silurian pod-shrimp *Ceratiocaris papilio* (≈2,356 per sq. mm), but closer to that for *Dithyrocaris insignis* (800 per sq. mm) (Rolfe 1962).

The epicuticle of *Cyclus* has structures similar to those of copepods. The pores on the surface are sparsely distributed amongst thread-like corrugations of the

cuticle (Laverack and Barrientos 1985, p. 132). These structures were found to be unique to *Cyclus* in this study (see Plate 5.12g).

Plate 5.13

a) Cuticular microstructure of an etched section of the carapace of *Tealliocaris robusta* from Bearsden (HM; X200, scale-bars=10μm). Open circle =recrystallized-phosphate, open triangle=pore canals.
b) Detail of the recrystallized-phosphate portion of the cuticle (HM; X3200, scale-bars=1μm).
c) Detail of the pore canals (open square) and tegumental duct (closed triangle) (HM; X800, scale-bars=10μm).
d) Detail of the pore canals showing helical structure (HM; X3200, scale-bars=1μm).
e) Close-up of the pore canals showing the mamillated surface texture (HM; X12500, scale-bars=1μm).
f) Different exposure of the above (e) to show that the pore canals are continuous (HM; X12500, scale-bars=1μm).
g) Broken section of the cuticle of *Tealliocaris etheridgii* from Glencartholm showing the exocuticle (ex), the endocuticle (en), and the line of emergence (arrowed) (HM; X1200).

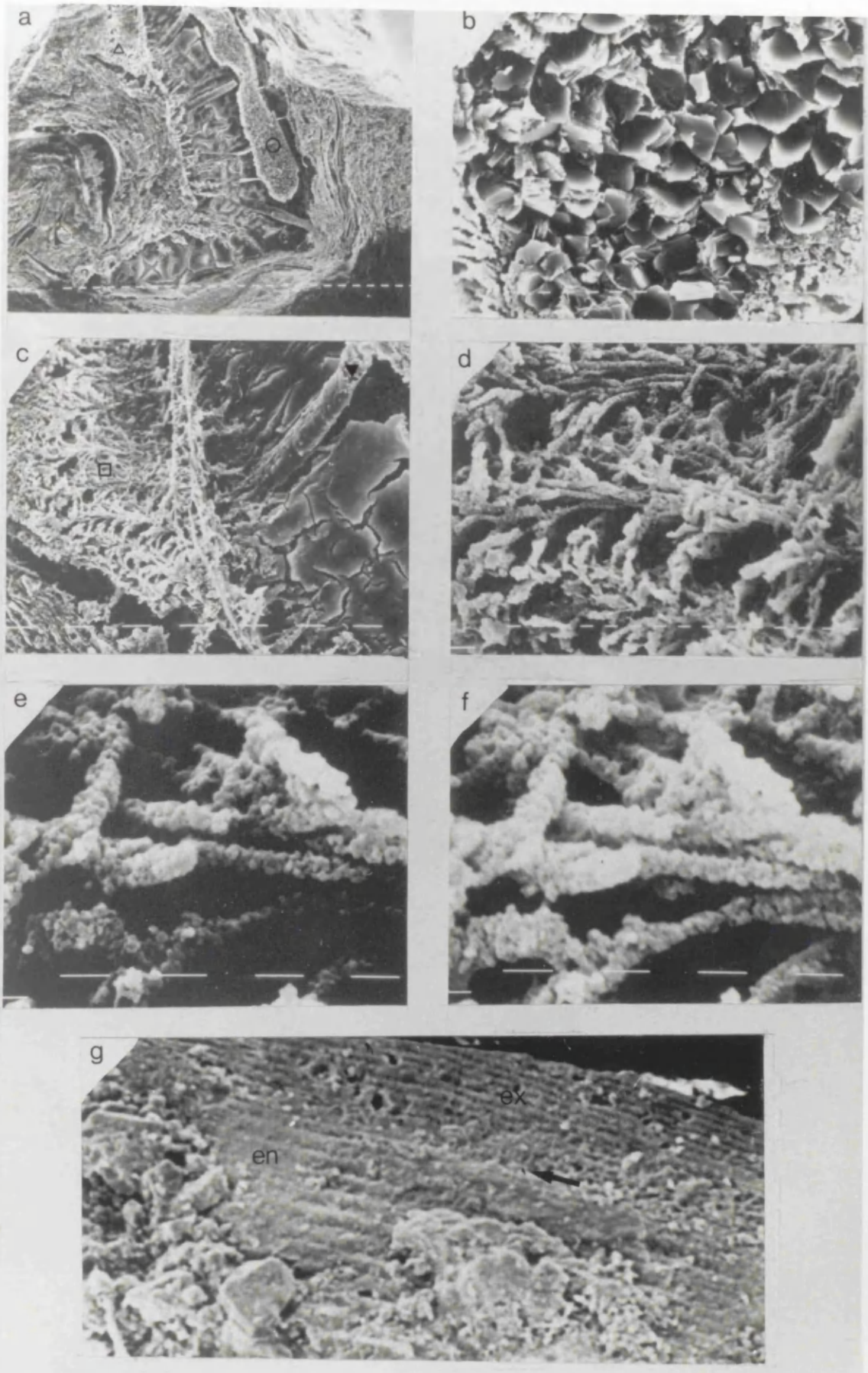

a
b
c
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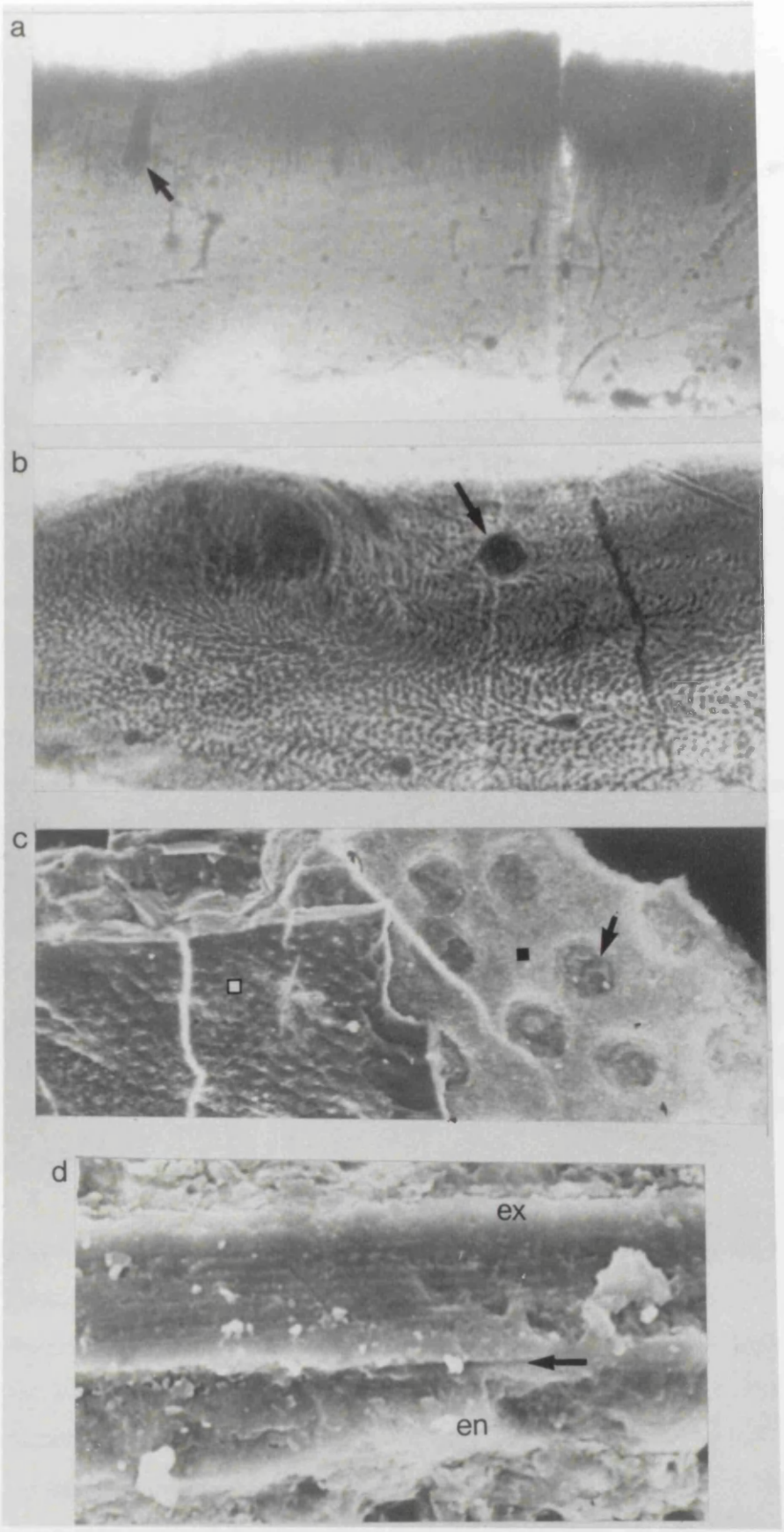
Plate 5.14

a) Thin-section in plane-polarized light of the cuticle of *Tealliocaris robusta* from Bearsden (HM; X385). Arrow points to a tegumental duct.

b) Oblique section through the cuticle of *Tealliocaris robusta* in plane-polarized light showing the arcuate nature of the pore canals (HM; X690). Arrow points to a tegumental duct.

c) Broken section of the cuticle of *Tealliocaris woodwardi* showing the surface of the epicuticle (white square) and the exocuticle (black square) (HM; X220). Arrow points to a tegumental duct.

d) Broken section of the cuticle of *Crangopsis eskdalensis* from Bearsden showing the exocuticle (ex), the endocuticle (en), and the emergence line (arrowed) (HM; X1700).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Chapter 6

Palaeoecology.

6.1 Palaeocommunities.

There have been many interpretations on what constitutes a biological community. To be able to discuss a fossil assemblage in terms of a community or communities, it is important to understand what a community represents in the ecological sense, and what limitations this has on palaeoecological interpretations. In an abstract form, communities may be based on general attributes, such as the recurrence of suites of species or the degree of interspecific interaction. More concisely, a community may be taken to represent an assemblage of organisms inhabiting a specific space (Johnson 1964). Communities, in an ecological framework, may be described in terms of the constituent species, numbers of individuals, biomass, and the proportion of various ecological roles represented (Johnson 1964). The boundaries of a community are usually poorly defined as many of the constituent species may freely mix with neighbouring communities (Kauffman and Scott 1976). It is inappropriate to apply biological community structure to most fossil examples as the many of the constituent species may not have been preserved. It is necessary, therefore, to erect a different set of parameters to define a palaeocommunity in order to show that it represents a part of a biological community.

Palaeoecological communities, or palaeocommunities, may be defined by detailed analysis of a fossil assemblage using criteria such as character species, recurring sets of species, dominant species, and the physiognomy of component species (Scott 1976). It is inappropriate, for example, to consider the ecology of Carboniferous shrimp-bearing shales holistically, as most of the soft-bodied animals are not preserved and it is difficult to assess which of the non-crustacean taxa were co-occurring with the crustaceans. To have been able to consider a palaeocommunity holistically it would have been necessary to study the total biotic composition, species interactions, and the interactions with the

environment (Kauffman and Scott 1976). It is important, however, to recognise that the palaeocommunity represents a part of a holistic ecological unit when considering the palaeoecological interactions of the constituent species. The result should be a hypothetical model describing the biotic interactions necessary to the existence of a community (Valentine 1973). One of the most important criteria in determining whether interactions between species may have taken place, is the identification of a recurring population of organisms over a geologically significant period of time, or a chronofauna (Olson 1952).

Other important features of community analysis include the evolution of the environment through time, the nature of the life cycle of individual organisms, and changes in the availability of nutrients. Time may represent anything from the seasonal variations of the environment to the longer time spans represented by features such as transgressions or regressions. This dynamic nature of palaeoecology can be observed in the study of sedimentary sections in detail. The changes in the environmental conditions are emphasized by the related changes in the diagenetic and taphonomic processes. This means that a change in the environmental conditions may not only affect the biotic composition, but may also affect the preservation potential of some of the individual taxa. In the case of the crustaceans, if they had not been affected by a phase of early phosphatisation then their preservation potential would have been greatly reduced. This is evident from the various states of preservation in the shales, and the rapid bacterial decay observed in modern crustaceans (Plotnick 1986, Allison 1988).

6.1.1 Definition of a palaeocommunity as related to the crustacean assemblages. For the purposes of this thesis a *palaeocommunity* will be defined as an assemblage of genera/species which are similarly preserved (undergone similar taphonomic and early diagenetic processes), and are found in association repeatedly within a single lithological unit representing a significant period of time. If an assemblage of species has been defined as a palaeocommunity at one locality, and the same assemblage of species is found elsewhere, then both these assemblages are considered to represent a palaeocommunity. These two palaeocommunities are unlikely to be part of the

same palaeocommunity, despite having the same constituent species, unless there is good evidence that one gave rise directly to the other. This can occur where the palaeocommunities belong to the same, or adjacent, palaeogeographical environment at an equivalent geological horizon.

If a group of organisms co-occur at only one locality in a thickness of sediment not considered to represent a significant period of time, then the group of organisms will be called an *assemblage*. If two, or more, geological horizons have the same, or similar, constituent genera/species but each horizon does not represent significant periods of time, the groups of organisms cannot be taken to represent palaeocommunities and will be called *parallel assemblages*. Palaeocommunities will be named first by the geographical area or locality name and then by the constituent taxa.

Palaeocommunities may be defined differently depending on the nature of the deposit and the constituent organisms. A significant period of time may be considered as being instantaneous when rapid burial or mass mortality occurs to preserve the palaeocommunity. It is more reliable, however, in the majority of cases, to define a palaeocommunity in terms of the persistence of a particular assemblage over a period of time. This would indicate that the assemblage of organisms was more likely to have interacted as a community.

The period of time which is considered to be significant is highly subjective, as a living community may represent a group of interacting organisms at any instant in time. In terms of the crustacean-bearing shales from the western Midland Valley of Scotland, one centimetre may represent 100 years, assuming that one lamination couplet (organic/inorganic) represents one year. During the excavation, collection and recording of faunas occurred every 0.5-2.0cm, providing a resolution of 50-200 years. A significant period of time, in this case, is taken to represent a period of greater than 200 years. The reason for assuming that each lamination represents one year is that the increased nutrient input into the area is likely to be due to an annual wet-season at higher latitudes, within the Laurasian continent, resulting in an increase in the river water volume entering the equatorial MVS.

6.1.2. Definition of the Western Midland Valley of Scotland Crustacean Palaeocommunity.

The crustaceans from the Shrimp Member of the Manse Burn Formation, used in this palaeoecological study, are all similarly preserved by phosphatisation events. These events occurred rapidly causing the phosphatisation of the crustaceans which lived together at any moment in time. There are also a large number of crustaceans which are less well preserved as a result of rapid bacterial decay to form radially crystallized microconcretions which are not included in the palaeocommunity as they were not present during eutrophication, which resulted in the phosphatisation events. Other crustaceans were not phosphatised and did not decay, but were affected by an early dissolution of the cuticle followed by a reprecipitation of drusy calcite in the resultant pore space. These non-phosphatised crustaceans are also not included in the palaeocommunity for the same reason.

Because of the different preservation, most of the other non-crustacean organisms have not been included in the palaeocommunity, but they have been considered in terms of the assemblage as a whole to demonstrate variations in the environmental conditions. Only in the case of facultative commensalists, such as *Leiopteria sp.* attached to the carapace of *Cyclus rankini*, can direct associations be made between different organisms which are differently preserved.

The crustaceans found within the Shrimp Member of the Manse Burn Formation may be considered to represent a palaeocommunity for the following reasons:

1) the constituent crustacean genera are similarly preserved by rapid phosphatisation,

2) the Shrimp Member is a single lithology representing a significant period of time (≈33600 years) in which the association of species is repeated,

3) the community is confined to a restricted geographical area interpreted as a back-barrier lagoon,

4) the same taxonomic association is also found in the Granton Shrimp Bed (Viséan) which, therefore, also represents a palaeocommunity (see section 6.1.1) (ie: given the same conditions, it is a repeatable phenomenon).

The palaeocommunity is called the *Western Midland Valley of Scotland Crustacean Palaeocommunity* and consists of the following crustacean genera which are thought to have lived contemporaneously within the back-barrier lagoon: *Crangopsis, Palaemysis, Tealliocaris, Cyclus*,and *Tyrannophontes.*

One other crustacean genus, *Minicaris*, is also found associated with the above community, but is not thought to have lived in association with the above crustaceans due to different preservational characteristics. This crustacean is, therefore, not considered as part of this community.

6.1.3 Palaeocommunity evolution.

Olson (1966) used the term 'community' in a very broad sense to show that the basic trophic structure and interactions remain constant in any environment through geological time. The survival of a community through geological time is not dependent on the biotic components as these die out to be replaced by taxonomically or ecologically equivalent taxa (Olson 1966). This must not be confused with faunal succession which is related purely to environmental changes over a shorter period of time in a particular area (M^{c}Call and Tevesz 1983). The recognition of similar faunal successions in different geological periods indicates similar environmental controls, and may be used as a tool in determining community evolution (Walker and Laporte 1970, Sepkoski and Sheehan 1983).

To determine the factors which would affect Western Midland Valley of Scotland Crustacean Palaeocommunity, it is necessary to look towards extant communities in similar latitudes where environmental seasonality appears to be the most significant factor. In the equatorial regions, solar radiation intensity does not vary much and is unlikely to affect communities directly. The distribution of the continents, however , will cause seasonal climatic pressure gradients due to changes in the solar radiation intensity. This in turn may cause changes in the velocity or direction of ocean surface currents (Valentine 1983). Temperature variations of the ocean surface waters in equatorial regions is quite small and therefore has little effect. Salinity variations may be quite

high due to freshwater incursions by rainfall or river transport, or by high rates of evaporation, and can severely affect benthic communities, although, benthic communities destroyed by freshwater influxes may return with the return of marine conditions. As the freshwater is likely to be richer in nutrients than marine waters, a seasonal influx of freshwater will produce a seasonal phytoplanktonic bloom.

Low species diversity occurs in areas of high seasonality, where there is a tendency for trophic generalists to survive best. The resulting communities are dominated by species feeding on the lower trophic levels (Valentine 1983). Competition and predation are important features of high and low-diversity communities. There is a relative increase in predator diversity in high-diversity communities presumably related to the increase in the number of trophic levels present (Valentine 1983).

Communities in nearshore situations appear to expand offshore through time due to extinction resistance, adaptation, and co-adaptation (Jablonski and Bottjer 1983, Sepkoski and Sheehan 1983). A generalist nearshore, therefore, becomes a specialist offshore. Individual taxa within a community may affect their own evolutionary and adaptive potential due to spatial variations in community composition, especially under stressful conditions (Wilson 1976). This would result in the community adapting to the individual, assuming a certain amount of control of the community over its component species.

In theory, therefore, palaeocommunities from different geological periods, assuming similar geographical environments and environmental seasonality, should exhibit similar trophic structure despite any taxonomic differences. This has been demonstrated by a study of similar environmental successions of Ordovician and Devonian communities where there had been substantial taxonomic changes (Walker and Laporte 1970).

As the taxonomic constituents of a community may be replaced by ecological equivalents which are not necessarily of the same taxonomic group, it is important not to restrict a study of community evolution to any single taxon.

The Western Midland Valley of Scotland Crustacean Palaeocommunity, however, does not exist elsewhere at a higher stratigraphical level. This would have been expected if the palaeocommunity persisted through time. The palaeocommunity must, therefore, have been dispersed preventing the persistence of this community through geological time.

6.1.4 Crustacean palaeocommunities and community evolution.

Schram (1981a) described four Carboniferous communities in which crustaceans were noted as the most significant component. Four crustacean feeding types were recognised to define the trophic structure of these communities, (1) rapacious carnivores, (2) low-level carnivores or scavengers, (3) filter feeders, and (4) detritus algal feeders and grazers. As Schram does not deal with the non-crustacean associated biota, it is not possible to construct a full picture of the community structures. Even if the other taxa were considered, it would be difficult to determine whether they formed part of the original interacting community.

Each individual crustacean taxon is assumed to belong to a single feeding type by Schram (1981a). This produces a false impression of the interactions between the crustaceans and the community, as a whole, as crustaceans may perform a number of feeding modes. *Procaris*, for example, is considered a facultative feeder as it feeds by passive predation, scavenging, and grazing (Provenzano 1978, Abele and Felgenhauer 1985). Of the palaeocommunity under consideration here, *Tealliocaris* may also have been a facultative feeder having similar limb morphology to *Procaris* (see section 5.6).

Although the taxonomy of the Carboniferous crustaceans is less well known than Schram (1981a) suggests, it is still possible to infer possible feeding habits, and hence trophic levels, from morphology. Many of the basic morphological characteristics relating to the feeding processes are known from previous descriptions of these fossil crustaceans (Peach 1908, Schram 1979, Schram 1981a), and it is possible to determine the feeding modes (Fig. 6.1) using

limb morphology, in a similar manner to that attempted by Schram (1981a). Schram (1981a) also suggests that the high-diversity crustacean faunas from 'near-shore' environments may have acted as a reservoir for some elements found in other environments.

Figure 6.1 Crustacean feeding types within the Shrimp Member.

Feeding type	Crustacean genera
Predators	*Tyrannophontes*
Scavengers	*Palaemysis*
Filter feeders	
and grazers	*Palaemysis*
	Crangopsis
	Cyclus
Facultative feeders	*Tealliocaris*
	Minicaris

The major factors affecting the recognition of crustacean community evolution include the preservation potential of the crustaceans, and the distribution of the continents from the Upper Devonian to Upper Carboniferous. Environments promoting the early diagenetic phosphatisation of crustaceans in restricted, low-energy bodies of water in equatorial and tropical regions became more common in the Carboniferous, prior to the closure of the sea-way between Laurasia and Gondwana in the Permian (Smith *et al.* 1973, Schram 1977). As a result of this increase in preservational environments, it appears as though there is a rapid radiation of hoplocaridans and eumalacostracans in the Lower Carboniferous, apparently evolving from a few poorly preserved genera in the Devonian (Schram 1977). It seems more likely that malacostracan crustaceans evolved more slowly from Lower Devonian ancestors which were not now preserved (see section 3.1).

In the Permian the crustaceans become less diverse consisting mainly of species from restricted environments. These become even rarer by the Triassic, although, decapod crustaceans from the marine environment become more common (Schram 1977).

The crustacean radiation in the Lower Carboniferous, coupled with the poor state of preservation of specimens before the 'radiation' and also from post-Carboniferous deposits, suggests that these observations are greatly influenced by taphonomic and early diagenetic preservation potentials, rather than relating to a true evolutionary feature of the communities or individual taxa. It is possible that these preservational environments did not exist, or were very rare, before and after the Carboniferous, or that the communities moved from and into environments where their preservation potential was greatly reduced. It is, therefore, not possible to study crustacean communities in terms of community evolution.

6.2. Palaeoecology of the Western Midland Valley of Scotland Crustacean Palaeocommunity.

Previous ecological studies of Carboniferous malacostracan crustaceans have centred on their trophic level and faunal associations, resulting in general concepts of their salinity tolerances (Schram 1981a). The salinity tolerances are usually discussed in terms such as, fresh to brackish (Baird *et al.* 1985, Clarkson 1985), marine (Briggs and Clarkson 1983, Baird *et al.* 1985, Cater 1987), non-marine (Copeland 1957), hypersaline (Dewey and Fåhraeus 1982).

It was noted by Schram (1981a) that several late Palaeozoic crustaceans could tolerate a number of different environments, as many crustacean species are found with in different associations. Hesselbo and Trewin (1984), for example, noted that *Tealliocaris* was an opportunist which proliferated in the favourable non-marine conditions at Gullane, but was found in much reduced numbers in more marine conditions at Granton.

To further constrain the physiological and environmental tolerances of the Carboniferous crustacean genera from the Shrimp Member, the autecology, synecology, and the distribution of these crustaceans are here discussed.

6.2.1. Synecology and distribution of the crustacean genera in the Western Midland Valley of Scotland Crustacean Palaeocommunity.

Synecology is the study of the relationship between communities and their environment (Bates and Jackson 1987, p668), and autecology is the study of the relationship between individual organisms, or species, and their environment (Bates and Jackson 1987, p45). The composition of the community is variable, as many of the genera are adapted to different broad environmental conditions which overlap. The environmental tolerances of the different genera can be interpreted from their faunal associations, and their distribution within the restricted area covered by the Shrimp Member. Although it is possible that the crustaceans studied from the Shrimp Member interacted as a community, it can be shown from their lateral distribution within the confines of the back-barrier lagoon, that the interactions were limited to areas where their environmental tolerances overlapped. The environmental tolerances of the crustacean genera from the Shrimp Member are discussed below in terms of the community as a whole and of each individual genus.

The environmental tolerances of *Tealliocaris* have been the subject of much controversy, as hypersaline lagoons to thermally stratified lakes have been suggested for this crustacean's life environment. *Tealliocaris* occurs abundantly at Gullane, but is associated with only rare ostracodes, fishes, hydroids, scorpionid fragments, and plant fragments (Briggs and Clarkson 1985a), whereas, at Bearsden and Granton, it is only a minor constituent of the fauna which consists mainly of other crustacean genera such as: *Crangopsis*, *Palaemysis*, *Tyrannophontes*, *Minicaris*, and others. At Glencartholm, near Langholm in Dumfriesshire, it is also a minor constituent, but is associated with a more diverse crustacean fauna. If *Pseudotealliocaris* is considered to be allied to *Tealliocaris* (see Chapter 5), then a more complete picture of the salinity tolerance of *Tealliocaris* emerges, as this genus appears at several localities in North America (Copeland 1957, Factor and Feldmann 1985, Schram 1988). The widespread distribution of this genus, the paucity of specimens from normal marine environments, and the abundance of specimens in high salinity environments supports the view of Hesselbo and Trewin (1984) that *Tealliocaris* was an opportunist. Hesselbo and Trewin (1984) suggested,

however, that the environment in which *Tealliocaris* is found at Gullane was that of a thermally stratified lake or brackish lagoon, rather than being hypersaline. The tropical position of the environment in which *Tealliocaris* lived, and the dolomitic composition of the sediments at Gullane, may support the more saline habitat suggested here. Dewey and Fåhraeus (1982) also suggest a preference for a hypersaline habitat for *Tealliocaris* from Lower Carboniferous of Newfoundland, although it was also found in small numbers in more normal marine environments.

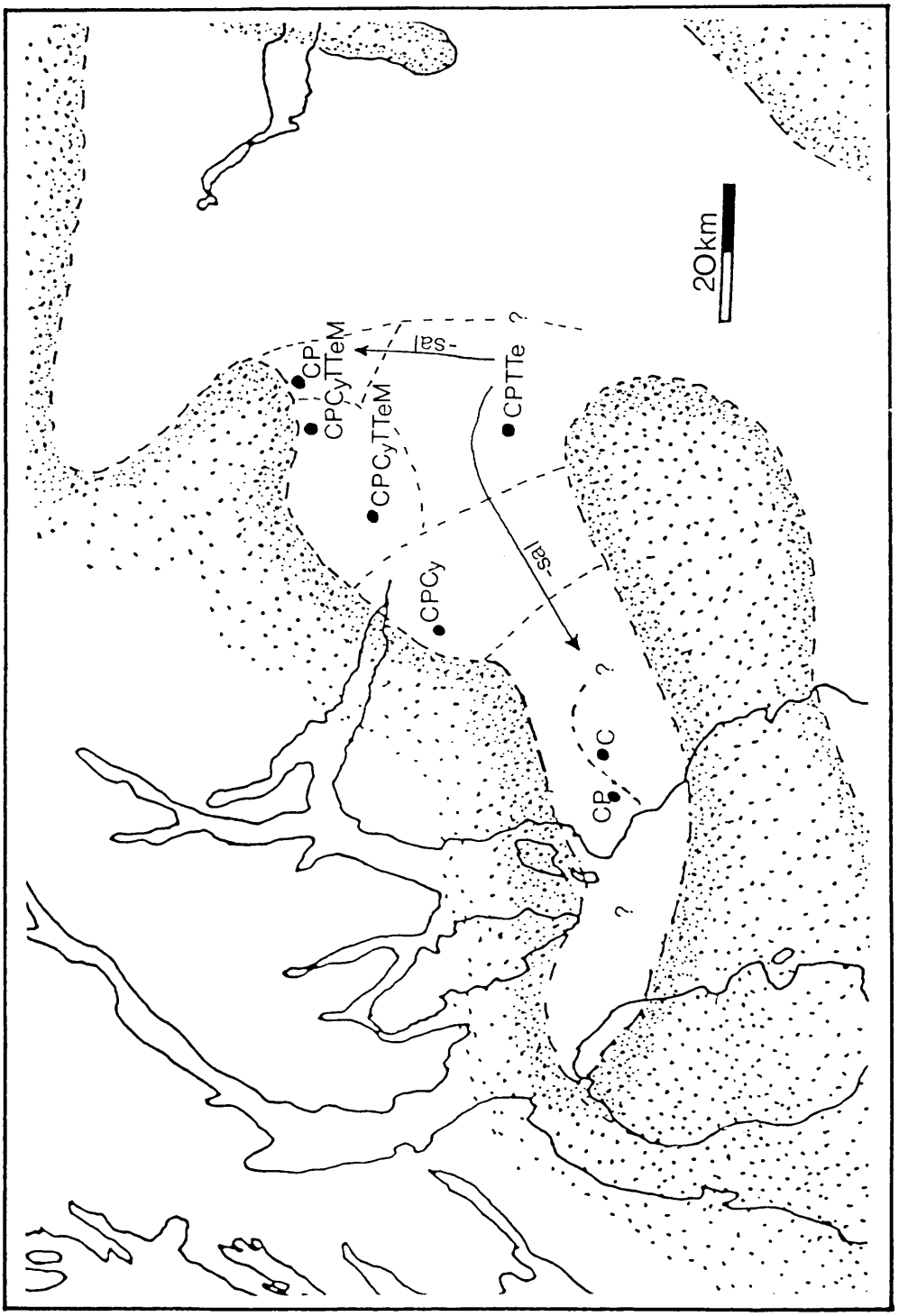
In the Shrimp Member of the Manse Burn Formation, *Tealliocaris* is a minor element of the fauna, and has only been found in the more eastern localities of Bearsden, Spouthead, and East Kilbride (Fig. 6.2).

Crangopsis is another Carboniferous crustacean which occasionally occurs mostly alone with only small populations of other faunal elements, such as in the sediments representing a brackish water environment at Ardross, near Elie in Fife (White 1937), or associated with a diverse crustacean fauna, such as at Glencartholm (Schram 1983). At Granton the dominant crustacean, *Waterstonella*, may be synonymous with *Crangopsis* (see Chapter 5) making *Crangopsis* the dominant genus also in environments of periodic normal marine salinities. It has not been recorded from freshwater environments, but is certainly found in brackish and marine environments. *Crangopsis* is unlikely to represent an opportunist genus, as it invariably dominates the communities whenever it occurs. This indicates that it had successfully adapted to a range of environmental conditions with no particular competitive restraints. It is, therefore, a euryhaline crustacean which was able to live in salinities lower than that tolerated by *Tealliocaris*. As it is not found in the extreme salinity conditions of freshwater or hypersalinity, it is unlikely that it was able to osmoregulate to the same degree as *Tealliocaris* and can, therefore, be considered as an osmoconformer relative to *Tealliocaris*.

In the Shrimp Member of the Manse Burn Formation, *Crangopsis* is found abundantly across the full extent of the area covered by this member. In the eastern portion, it is found associated with the more diverse crustacean fauna,

and in the west, it is found with only the abundant bivalve spat characteristic of the Shrimp Member across the lagoon (Fig. 6.2).

Figure 6.2 Map of the crustaceans distribution within the lagoon (C=*Crangopsis*; P=*Palaemysis*; Cy=*Cyclus*; T=*Tyrannophontes*; Te=*Tealliocaris*; M=*Minicaris*; arrows and -sal indicate the direction of decrease in salinity).



In the case of *Palaemysis*, and *Tyrannophontes*, the salinity ranges tolerated by these two genera appears to be quite small. *Palaemysis* is rarely found alone and is most commonly associated with *Crangopsis*, *Tealliocaris*, and palaeostomatopods, as well as other crustaceans at Bearsden, Glencartholm (Peach 1908), and Granton (Briggs, Clarkson, and Clark *in prep.*). It seems likely that *Aratidecthes* and some forms of *Anthracophausia* are synonymous with *Palaemysis* (see Chapter 5) which would extend the range of *Palaemysis* into North America. *Palaemysis* and *Tyrannophontes* occur together in the Shrimp Member, although in different abundances, suggesting that their salinity tolerances are quite similar, although their trophic levels are quite distinct. As they both appear to occur in environments influenced by waters of near normal marine salinities and nowhere else, their salinity tolerances are interpreted as being of a narrow range. *Tyrannophontes* is, therefore, considered to be stenohaline relative to the other Carboniferous crustaceans under consideration here. As it has such a narrow salinity tolerance range, it is not possible to comment on its osmolality as it could have limited osmoconformable or osmoregulatative capabilities.

Palaemysis is an abundant member of the crustacean community of the Shrimp Member, and is found at most localities, except in the western-most locality of the Powgree Burn. *Palaemysis* also becomes less common towards the west (Fig. 6.2). The abundance of *Palaemysis* in environments considered to be of lower salinity, suggests that it was euryhaline, and possibly an osmoconformer.

Tyrannophontes has been recorded only from three eastern localities at East Kilbride, Bearsden, and Spouthead. As only three specimens have been obtained during the course of this study, it is difficult to place any special significance on this distribution. The small number of specimens, and the morphology of this animal suggest, however, that this animal was an active predator. Its morphological similarity to the extant mantis shrimps (Stomatopoda) suggests a similar predatorial mode of life.

Minicaris is problematic in terms of its lateral distribution within the Shrimp Member, and with its relationship to the Western Midland Valley of Scotland

Crustacean Palaeocommunity, as it occurs only in the north and northeastern localities at Bearsden and Spouthead (Fig. 6.2). It appears to be more common at the Spouthead localities (four specimens) than at Bearsden (six specimens), when the relative sizes of the excavations are taken into account. As the morphology of *Minicaris* is similar to that of the extant syncarid crustacean *Anaspides tasmaniae*, it is possible that it lived in a similar manner. *Anaspides* is a detritus feeder as well as being a predator, and lives in freshwater streams and lakes (Manton 1930, Schram and Schram 1974). Streams, or rivers, to the north, entering into the back-barrier lagoon during the deposition of the Shrimp Member, may have transported *Minicaris* in during periods of higher freshwater influence. The presence of a syncarid in an environment dominated by marine waters, does not preclude the possibility of it being transported, especially when the state of preservation is different. *Minicaris* has a much lighter coloured phosphate and tends to be greatly pyritised, whereas, the other crustaceans have a dark phosphate and very little, if any, pyritisation.

The fossil copepod genus *Cyclus* is found in both coral reefs and laminated shales, suggesting a mobile mode of life, despite its discoid shape and grasping limb morphology (see Chapter 5). The distribution and morphology of *Cyclus*, suggests that it lived epifaunally on floating algae, or debris, within the marine environment. It is found in the more diverse marine crustacean associations within the shales of the Shrimp Member and does not appear in the more remote parts of this member to the west (Fig. 6.2).

6.2.2. Salinity tolerances of fossil crustaceans from the Shrimp Member.

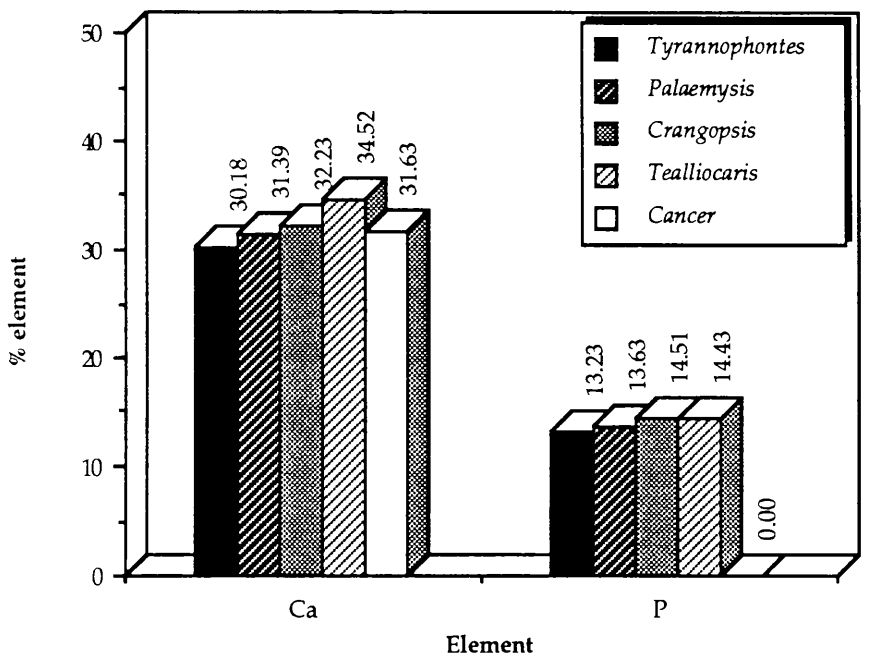
The relationship between the fossil crustaceans of the Shrimp Member and the surrounding environment, is discussed here in terms of the chemistry of the cuticle, but also, taking into account the evidence provided by the synecology, the autecology, and the distribution of these crustaceans (section 6.2.1).

The chemistry of the cuticle has not changed much from its original composition, due to rapid fixation during phosphatisation (section 4.1). Many of the elements found in the fossil cuticle are found in similar concentrations in

the cuticle of extant crustaceans (Fig 6.3). As the phosphate ions appear to substitute only the carbonate ions in the original cuticle, other elements, such as sulphur, chlorine, iron, magnesium, and sodium do not appear to be affected by the phosphatisation. It is unlikely that the elements derive from diffusion from the sediments, as the sediments and the fossil cuticle do not exhibit the same relative concentrations (Fig. 6.4).

Figure 6.3 The %element concentrations in the cuticle of some Carboniferous Crustacea compared with the extant crustacean, Cancer (a-calcium and phosphorus; b- minor elements).

a)



b)

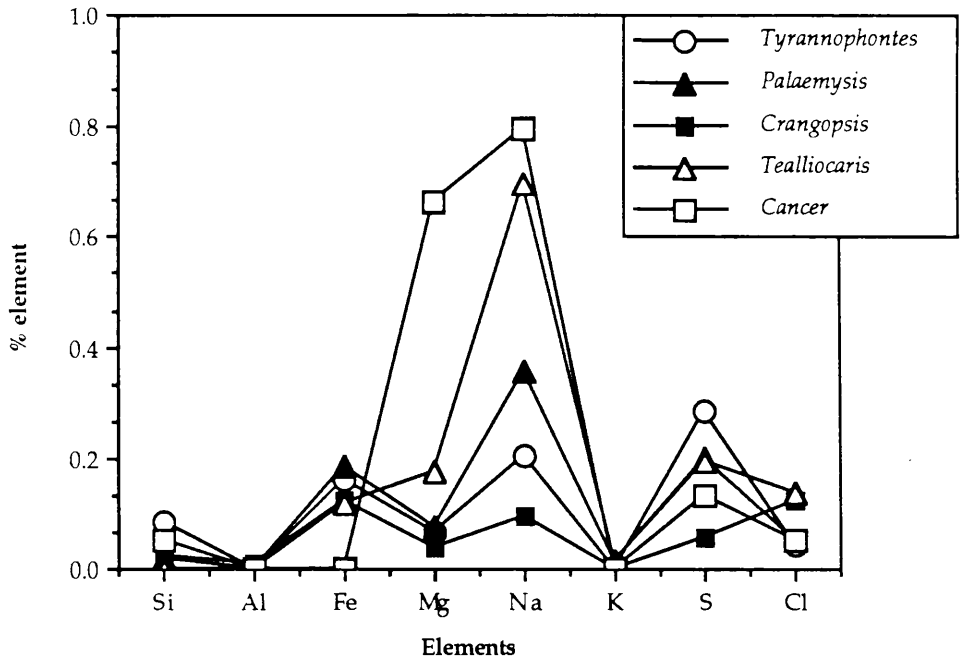
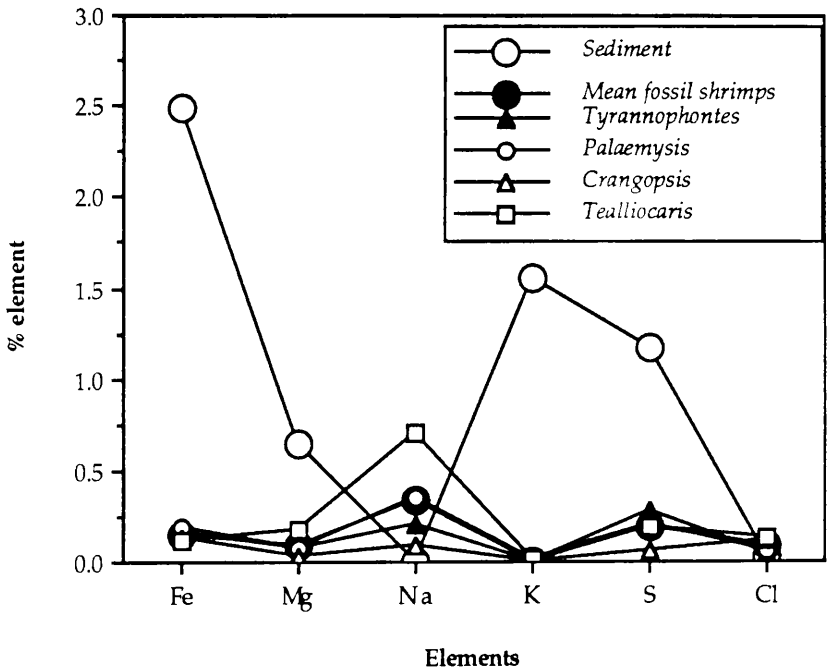
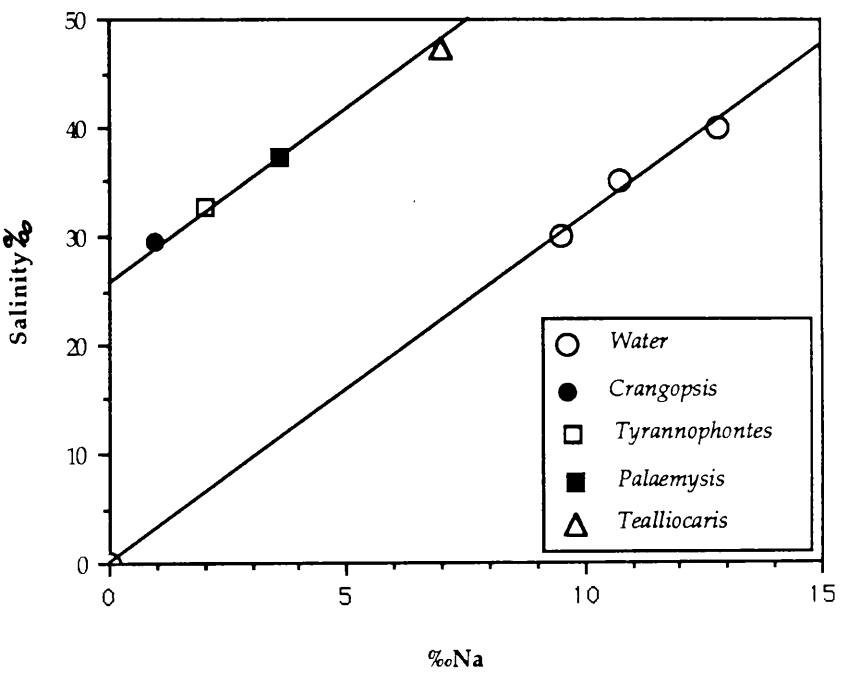


Figure 6.4 Graph showing the distribution of minor elements in the sediment surrounding the fossil crustaceans from Bearsden, in the calcareous nodules, and the mean crustacean composition.



The relative concentrations of these elements may reflect the environment in which the calcification of the cuticle took place (Fig. 6.5). The relationship between the concentration of these elements in the cuticle at the time of formation of the cuticle and the concentrations in the body fluids has not been established. The level of sodium in the cuticle of these crustaceans, however, correlates well with the inferred life environments, assuming environmental conditions which are near-normal marine salinity for *Tyrannophontes* and *Palaemysis* (Fig. 6.5) based on faunal evidence. The higher concentration of sodium in the cuticle of *Tealliocaris* may reflect the need, or the ability, to decrease the amount of sodium in the blood more than *Crangopsis*, *Tyrannophontes*, or *Palaemysis* do, or can.

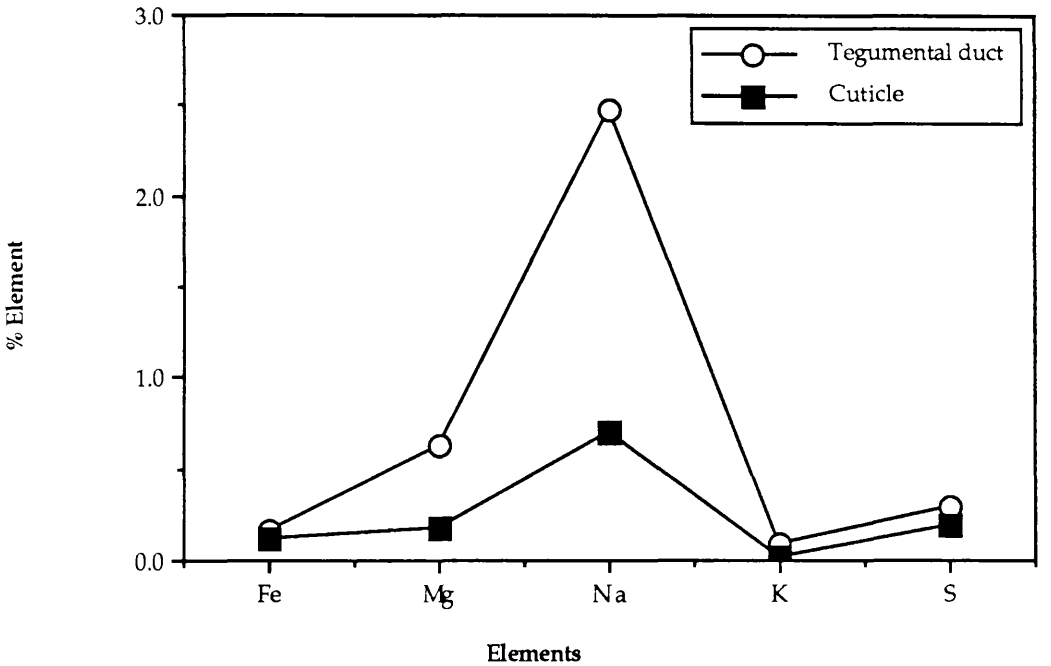
Figure 6.5 Relationship between salinity and sodium concentration assuming that *Palaemysis* and *Tyrannophontes* lived in waters of near-normal marine salinities, and that the slope of sodium concentration to salinity was the same in the Carboniferous as it is now.



This suggests that *Tealliocaris* is best adapted to living in more saline

conditions than the other crustaceans and is therefore considered to be a hyporegulator. The hypersaline tolerance of *Tealliocaris* has been previously proposed by Dewey and Fåhraeus (1982) although tolerance of low salinities has also been suggested (Hesselbo and Trewin 1984). The higher concentration of elements such as magnesium and sodium in a tegumental duct of *Tealliocaris* indicates that these structures may have been used in the transport and efflux of salts, although this increased concentration may also be secondary as a result of partial decomposition of organics within the tegumental duct and the inward diffusion of phosphate and sodium rich waters from the surrounding water column (Fig. 6.6).

Figure 6.6 Concentration of elements in a tegumental duct relative to the surrounding exocuticle of *Tealliocaris*.



The low sodium and sulphur content of the cuticle of *Crangopsis* suggests that it was better adapted to brackish and marine salinities (Fig. 6.3, 6.5).

The concentrations of sodium in the cuticle of the crustaceans analysed, relative to the salinity of the surrounding water may not have the same slope as present-day sea water, although, the trend is likely to be the same: the more

sodium in the cuticle, the more saline the surrounding waters (Fig. 6.5).

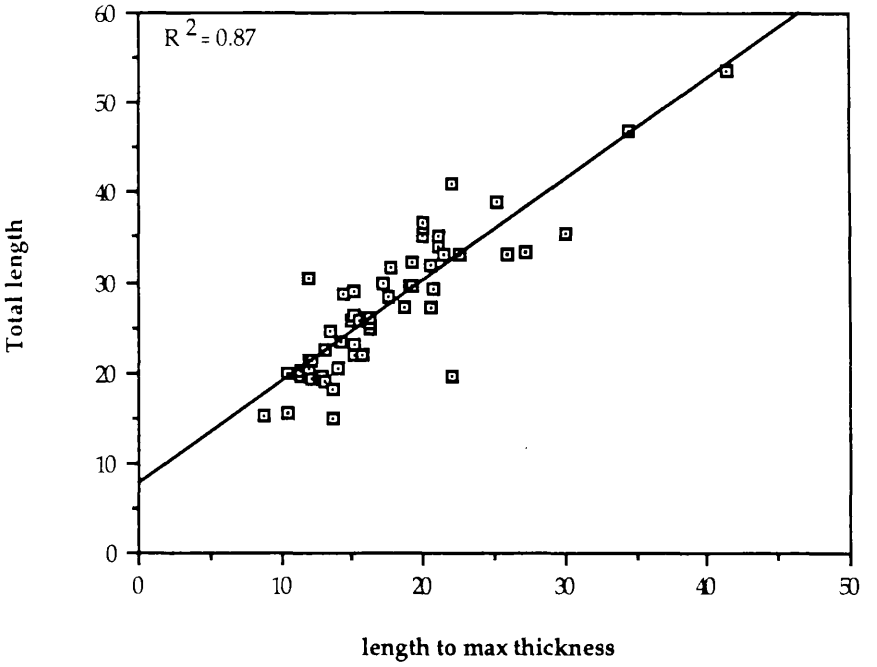
6.3. Interspecific interactions, or, coprolites and enterospirae.

The coprolites and the enterospirae are important factors in determining the interaction between the different animals within the back-barrier lagoon of the Western Midland Valley of Scotland Crustacean Palaeocommunity. The contents of these fossils can provide much information on the diet of the animal which produced them and, therefore, which animals existed in the lagoon at the same time. It is likely that the larger enterospirae belonged to fish and sharks, and the smaller amphipolar coprolites belonged to crustaceans.

6.3.1. Classification of coprolites and enterospirae.

A coprolite in the strictest sense is applied to fossilized excrement of animals (Häntzschel et al. 1968). It has also been applied to the fossilized gut contents of vertebrates (enterospirae) which have previously been considered as excrement (Buckland 1829). The origin of spiral "coprolites" was disputed by Agassiz as early as 1841 where he described them as cololites. Duverney (1844) noted that only animals in which the urine exits separately from the faeces could the excrement have the firmness to allow preservation of structure. He concluded that "coprolites" filled with bony material would easily disaggregate and spiral "coprolites" must, therefore, derive from dead and decomposed animals with spiral guts. Hoernes (1904) discussed two types of coprolites, the heteropolar and the amphipolar. The heteropolar coprolites are those with the external spiral structure concentrated at one end, and the amphipolar forms are those with no preferred polarity of external structure. The spiral excrement of the lungfish *Protopterus annectans* is amphipolar. Williams (1972) suggests that all amphipolar coprolites are true excrement and that the heteropolar forms represent enterospirae. The internal structure of the coprolite matrix is similar to the mucosal folds of the gut lining in extant animals (Williams 1972, Stewart 1978). The compact heteropolar forms from Bearsden appear to have formed from a consistent gut-shape and may derive from similar, or related, animals (Fig. 6.7).

Figure 6.7 Graph showing the strong external morphological similarity between compact heteropolar enterospirae.



6.3.2. Enterospirae and coprolites from Bearsden.

From the collection of "coprolites" from the Bearsden excavation, three basic forms have been observed:

1) compact heteropolar,

2) distended heteropolar, and

3) amphipolar.

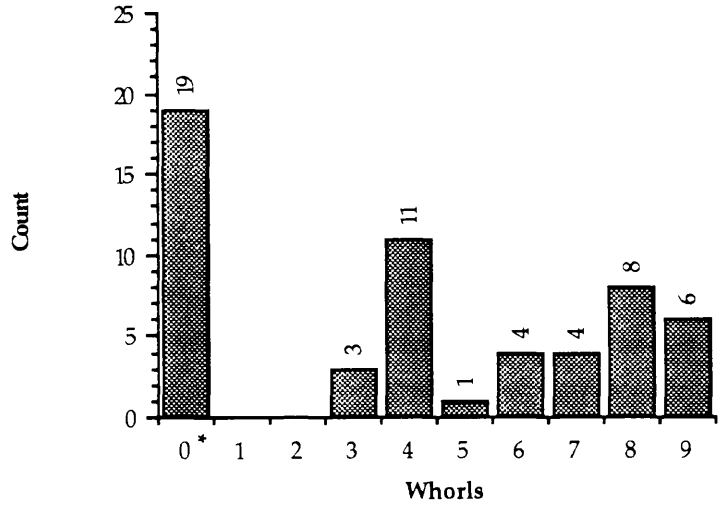
The vast majority of those collected are of the compact heteropolar form and one distended heteropolar form was found. A number of microscopic amphipolar or structureless coprolites collected from shale residues may represent crustacean pellets (Plate 6.1j).

Distended heteropolar (Plate 6.2a): The distended heteropolar enterospire resembles closely the gut form of the modern *Petromyzon* (Romer 1945). The gut of *Petromyzon* is a long thin twisting striated spiral quite unlike that of the

overlapping spiral structure of the modern shark *Scyllium* (Williams 1972). It is thought that this specimen represents the fossilized gut fill of a vertebrate with close affinities with the modern lampreys. This single specimen does not appear to contain any animal debris.

Compact heteropolar (Plate 6.1a-i, 6.2b): Of the compact heteropolar enterospirae, the fossil content appears to affect the state of preservation of the internal structures. It is considered that all 92 specimens examined were originally spiral of which 60% have retained a spiral structure to some extent. The remaining 40% have collapsed, and have not retained any of the original spiral structure. On the basis of the number of whorls, counting the maximum from the centre to the outer edge, two distinct groups can be seen. One group has only four or less whorls and another peaks at eight (Fig. 6.8)

Figure 6.8 Number of whorls in X-section of compact heteropolar enterospirae from Bearsden.

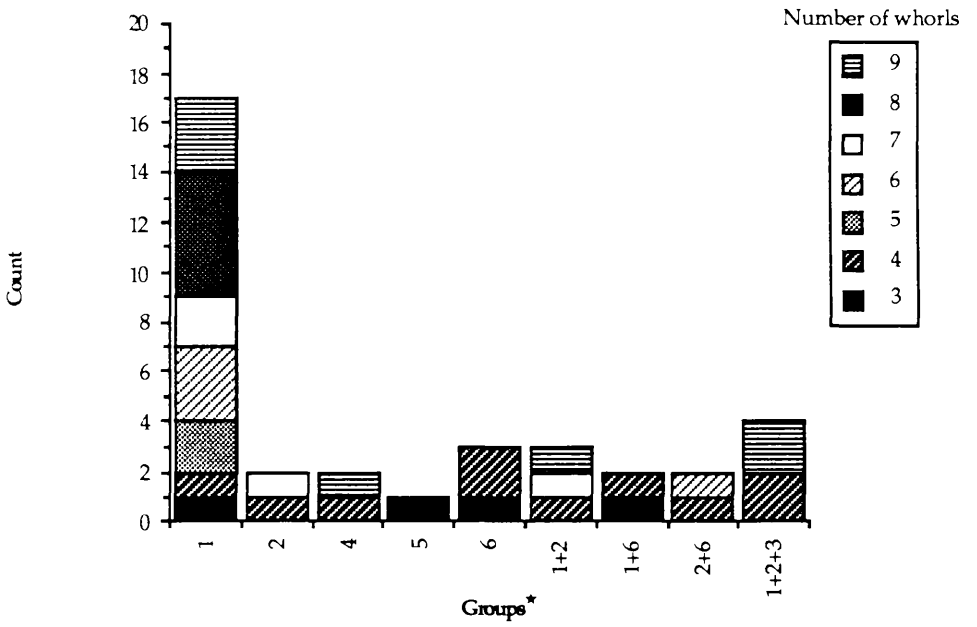


*collapsed coprolites and those with indistinct whorls.

6.3.3. Faunal composition of the enterospirae.

There does not appear to be any consistent correlation between the diet of the animal which produced the enterospirae, and the number of observed whorls (Fig. 6.9).

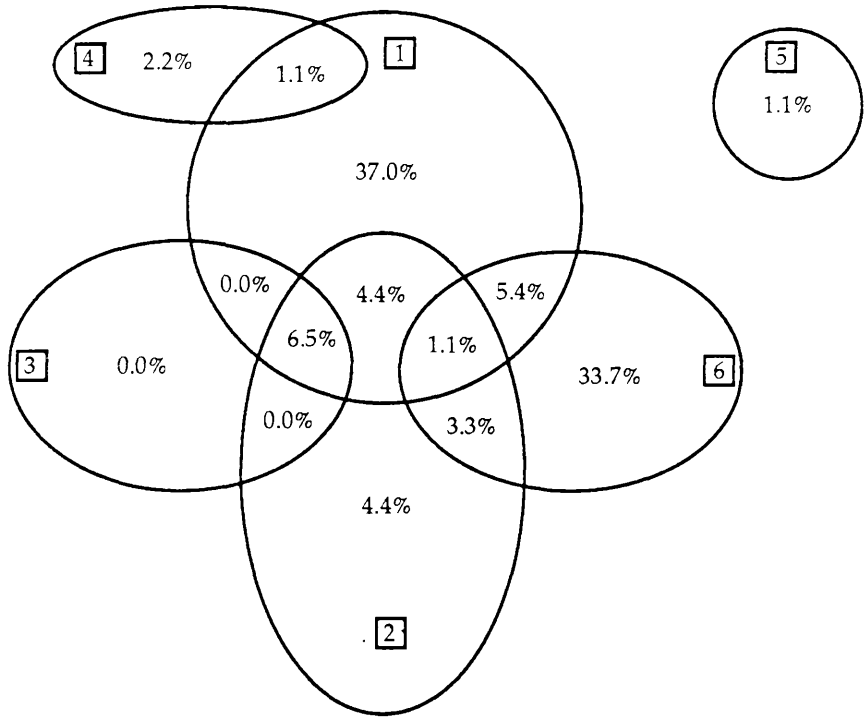
Figure 6.9 Histogram showing the relationship between the number of whorls and the diet contained within the enterospire (N=36).



*1: Palaeoniscid scales; 2: Acanthodian scales; 3: bivalves; 4: crustacean debris; 5: plant debris; 6: ultra thin ?fish scales.

The contents of the enterospirae include much of the observed fauna from the sediments, although not in the same concentrations. The contents of the enterospirae give an indication of what the animals of the higher trophic levels fed on, and hence the palaeoecological associations of these animals. It is likely that some of these enterospirae are from scavengers or deposit-feeders such as those which contain a number of different components, especially those which contain abundant bivalves. The enterospirae of predators are represented by those containing a more specialized diet of one or two species of animal, parts of which are found abundantly within the enterospirae (Fig. 6.9, 6.10, 6.11).

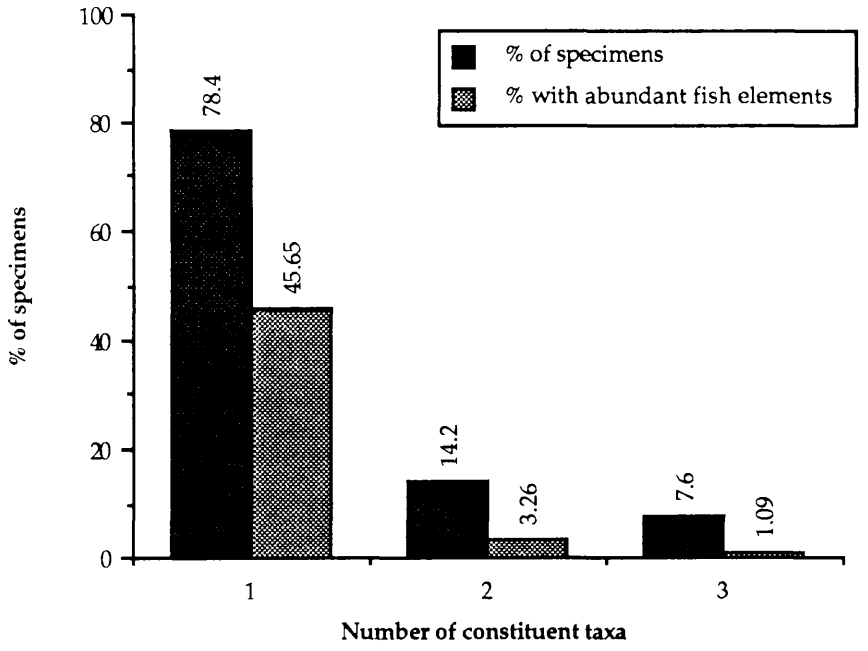
Figure 6.10 Enterospiral dietary contents in terms of % of specimens containing each fossil group 1-6* (*see Fig. 6.9) (N=91).



Groups which include only one fossil constituent are probably predators. It is possible that the enterospirae do not represent the remains of just one meal although, if the predator was in the process of digesting more than one catch, the gut would be packed with abundant fragments of its prey. Many of the enterospirae contain only a few scales indicating that these either belong to scavengers, or that the last meal of the predator had already mostly passed through the gut prior to the death of the animal. Possible predators include *Stethacanthus*, the palaeoniscids, the rhizodonts, and *Amphicentrum*. There are a few large enterospirae which are likely to belong to *Stethacanthus*, one of which is associated with a complete specimen (Hunterian Museum V.8246), another contains plant fragments and is rich in pyrite (NCB2) representing a possible vegetarian. The enterospirae which contain bivalve remains are found also to contain palaeoniscid and acanthodian scales indicating a non-specialized diet and probably belonged to a scavenger or an omnivorous predator.

The presence of the bivalves with the shell preserved also indicates that the animal to which the enterospirae belonged had either an alkaline stomach, or none at all. Four of these six enterospirae contain abundant bivalves (Fig. 6.10). The fishes which lack a stomach include the cyclostomes, chimeras and lungfishes. *Deltoptichius*, of which two were found amongst fifteen specimens of *Stethacanthus*, may have fed by scavenging and, on decomposition, released the enterospirae containing bivalves, acanthodian scales, and palaeoniscid scales. *Deltoptichius* is thought to be related to the modern chimeras (Dick *et al.* 1986).

Figure 6.11 Histogram showing the relative % of enterospirae containing 1-3 taxa and the % of the total with abundant fish elements (possible predators).



The majority of enterospirae contain abundant fish debris and also contain only one taxon. The abundance of scales from an individual fish within the enterospire suggests that the host animal was a predator, rather than a scavenger which would contain a small number of fragments of one or more taxa. The large number of enterospirae with abundant fish debris indicates that the majority of enterospirae derive from predators (Fig. 6.11).

6.4. Vertical faunal variations within the Manse Burn Formation.

An estimate of the relative changes in the proportion of different taxa within the Manse Burn Formation was produced to provide a guide to the overall environmental changes which occurred throughout the section. Orientation data for crustaceans in the Shrimp Member, and orthocones and sharks in the Posidonia Member, provide further evidence on the prevailing environmental conditions during the deposition of these shales (Wood 1982).

A more detailed example of the vertical environmental changes is given for part of the Shrimp Member, as a result of data obtained during the major excavation at Bearsden.

6.4.1. Faunal variation and environmental changes within the Manse Burn Formation.

The palaeoecology of the Top Hosie Shale has been studied in detail by Craig (1954) from a point below the Top Hosie Limestone at a locality near Kilsyth. He concluded (p116) that the environmental conditions, during the deposition of the Top Hosie Shale, were those of a low-energy shallow subtidal environment represented by two fossil communities: the *Posidonia* community and the *Lingula-Nuculopsis* community. The *Posidonia* community existed during periods of lower current activity and when the muddy substrate appeared more anaerobic, than when the *Lingula-Nuculopsis* community existed.

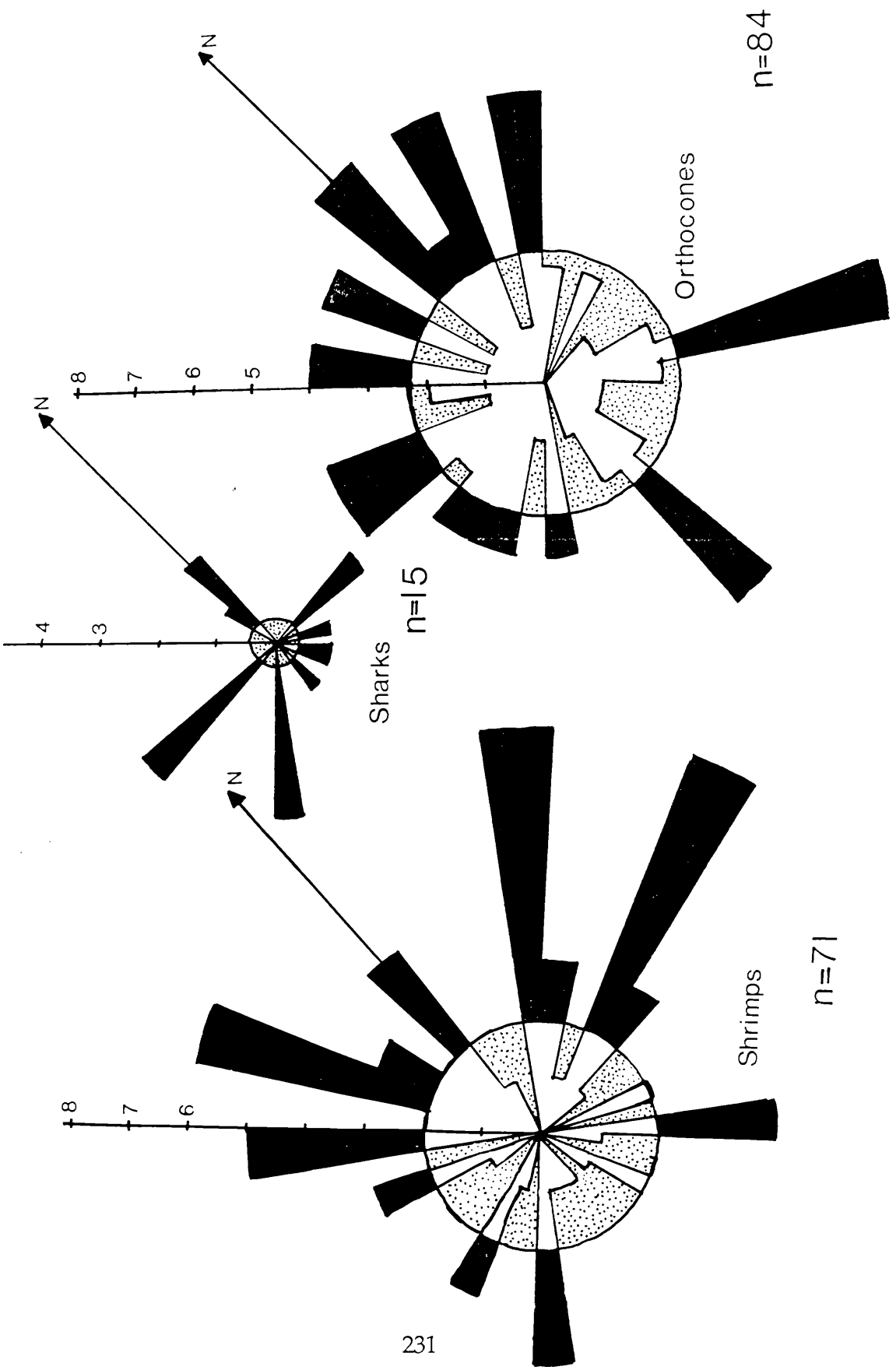
Immediately above the Top Hosie Limestone, the marine shale contains much the same fauna as the limestone and the marine shales below (0-20cm on figure 6.13). This is succeeded by less calcareous shales containing the restricted fauna of the Shrimp Member (20-300cm on figure 6.13). Although the Shrimp Member contains a large number of crustaceans, the most abundant fossil is the spat of a bivalve (possibly *Nucula*). Other faunal elements include myodocopid ostracods, which are common at the base of the Shrimp Member, but become less

common towards the top, and rare fish. Low-oxygen or anaerobic bottom water conditions have prevented the successful colonization of the substrate surface by sessile benthic organisms. The current energy was low enough to allow many of the crustacean carcasses and moults to remain articulated. The currents also do not show any preferred orientation (Fig. 6.12).

Posidonia occurs abundantly at one level within the Manse Burn Formation and also in the Top Hosie Shale below (Craig 1954). It occurs abundantly in the Posidonia Member (300-348cm on figure 6.13), associated with abundant gastropod and bivalve spat, orthocones, and conodonts, which may indicate oxic bottom waters with more open marine influence. This member also yielded the majority of the fish and sharks which were recovered during the major excavation (Wood 1982). The orientation data provided by the orthocones and the sharks show no preferred orientation, indicating a low energy environment (Fig. 6.12). A thin shale immediately above the Posidonia Member which contains *Minicaris, Palaemysis, Crangopsis, Cyclus,* and *Lingula,* was recorded by Wood (1982), but was not found during the course of this study.

The possible modes of life of *Posidonia* have resulted in much discussion (Jefferies and Minton 1965, Wilson 1966). *Posidonia* may have been a free-swimming pelagic bivalve as it is commonly found in toxic anaerobic sediments, and there is no evidence for attachment to floating debris (Jefferies and Minton 1965). Craig (1954) and Wilson (1966) suggested that it may have been a benthonic bivalve, with the capability of swimming, as the bottom waters may have been oxic despite the anaerobic sediments.

Figure 6.12 Rose diagrams showing orientation data for *Palaemysis* (Shrimp Member), Sharks (Posidonia Member), and orthocones (Posidonia Member) (inner circle represents the random distribution case).



The Nodular Shale Member (348-435cm on figure 6.13) has very few macrofossils except for the occasional bivalves, *Lingula*, plant fragments, fish scales, and very rare crustaceans. The environment represented is thought to be largely non-marine with a greater terrestrial input than with the previous members.

The Platey Shale Member (435-463cm on figure 6.13) contains rare bivalves, nautiloids, *Lingula*, disarticulated fish, conodonts, crustaceans. Bivalve spat, similar to that found in the Shrimp Member, and gastropod spat occur abundantly. Wood (1982) also recorded *Posidonia* from this horizon. This member is similar in character to the Posidonia Member and, presumably, represents a further minor marine transgression

The Betwixt Member (463-543cm on figure 6.13) contains occasional solitary bivalves and ostracods. The character of this member is similar to that of the Nodular Shale Member, although, there are fewer fossils. The environment of deposition is thought to have a more non-marine character with a significant terrestrial influence.

The Lingula Member (543cm-end on figure 6.13) contains a fauna of *Lingula* and *Naiadites* along with rare eumalacostracan crustaceans. A 0.2cm '*Crangopsis* marker band' (Wood 1982) occurs near the base of this member. Conodonts have been found associated with *Crangopsis* in the marker band. This member appears to represent a longer period when the shales were generally more aerobic and affected by slightly stronger currents, similar to the environment in which the *Lingula-Nuculopsis* community lived (Craig 1954). The environment was probably marginally marine with fluctuating salinities. The '*Crangopsis* marker band', which is only one lamination thick, may represent a period in which the bottom waters were less oxic and with little current activity to allow the crustaceans to be preserved.

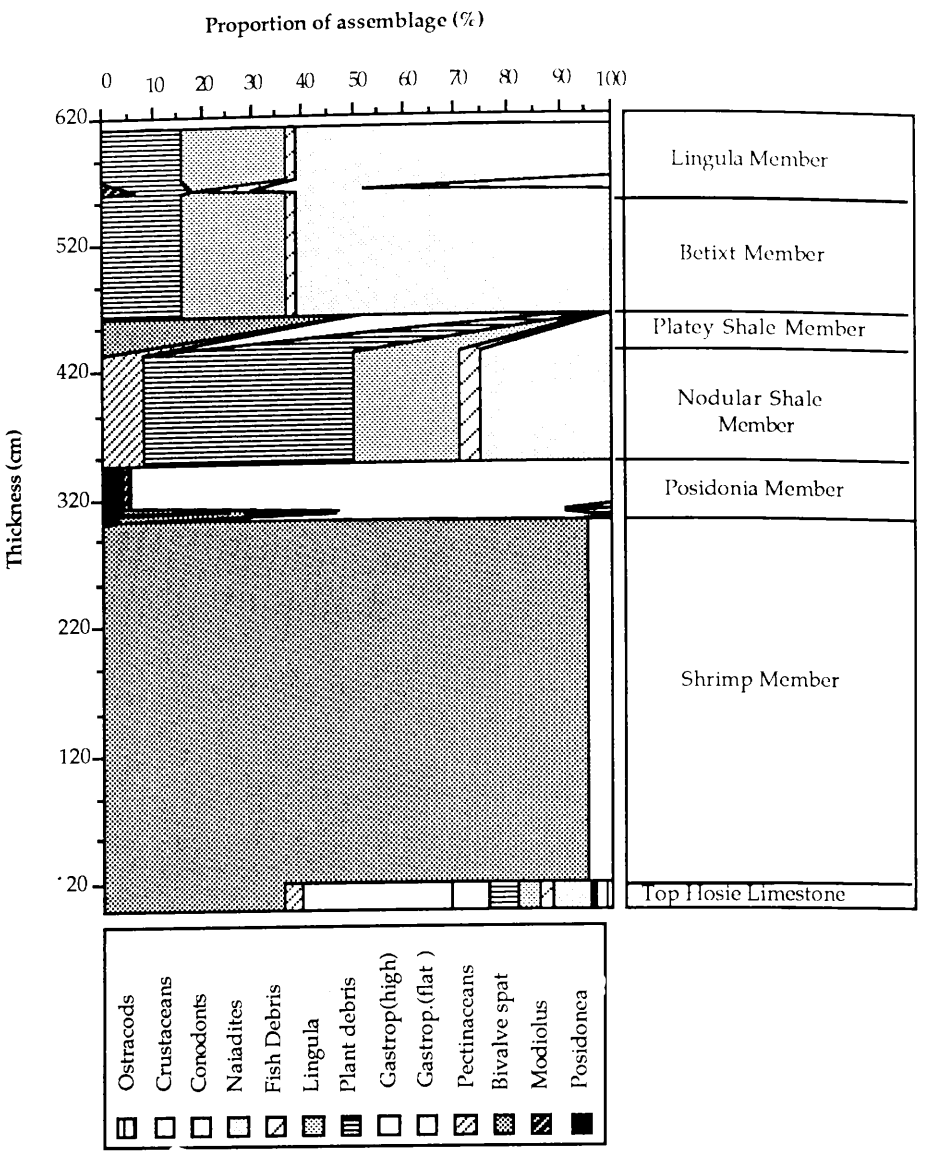

Proportion of assemblage (%)
0
10
20
30
40
50
60
70
80
90
100
Thickness (cm)
620
520
420
320
220
120
20
Lingula Member
Betixt Member
Platey Shale Member
Nodular Shale Member
Posidonia Member
Shrimp Member
Top Hosie Limestone
Ostracods
Crustaceans
Conodonts
Naiadites
Fish Debris
Lingula
Plant debris
Gastrop(high)
Gastrop.(flat)
Pectinaccans
Bivalve spat
Modiolus
Posidonca

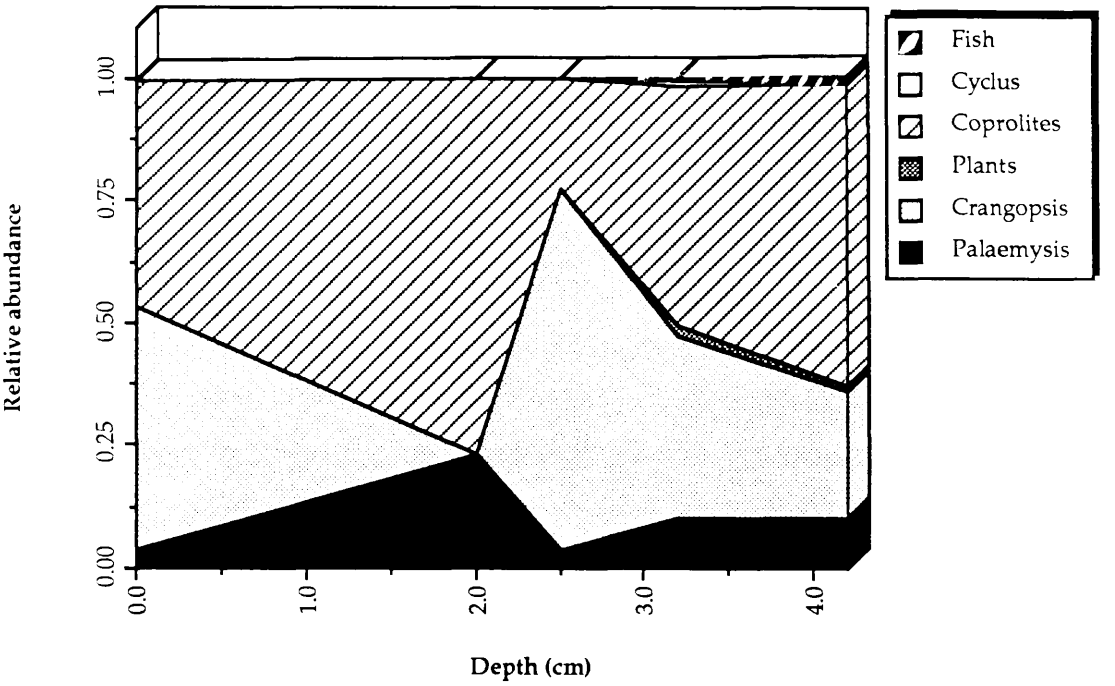
Figure 6.13 Diagram showing the change in fauna from the marine shale above the Top Hosie Limestone (0-10cm) to the Lingula Member (620cm) at the type locality for the Manse Burn Formation at Bearsden. (see opposite)

Above the Lingula Member the sediments become mostly barren in terms of their macrofossil content and gradually increase in sediment grain size from the shales into a mature sandstone. Most of these sediments represent the silting-up of the lagoon as it becomes more terrestrial.

6.4.2. Faunal variation and environmental changes in a measured section of the Shrimp Member.

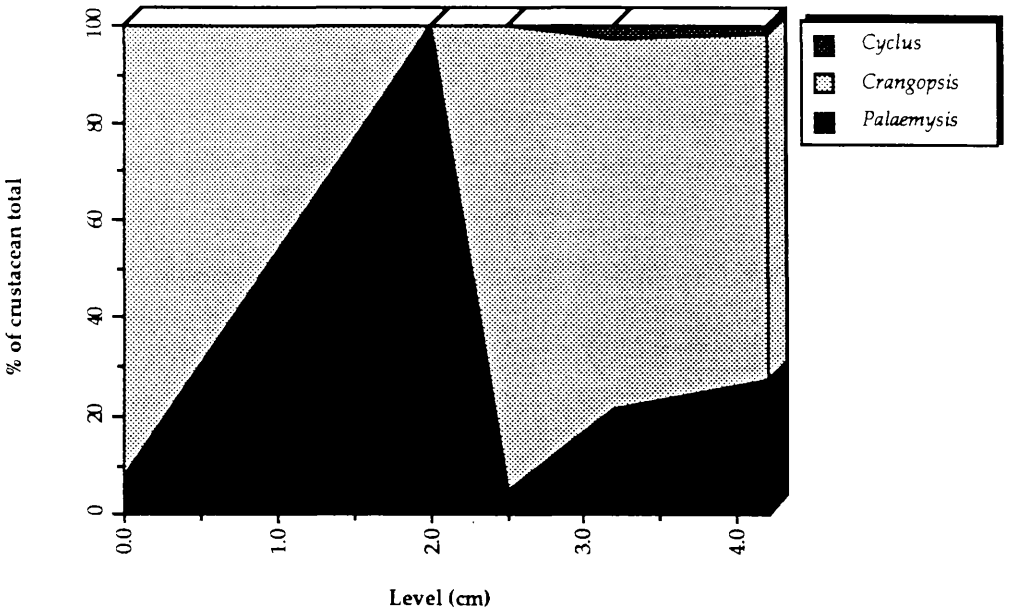
During the excavation of the Bearsden locality from 1981-1982, a detailed record of the relative position of the fauna within the Shrimp Member was made. Fourteen randomly selected square metres were selected for detailed faunal analysis, from seventy-five metres square. The thickness of the shales examined was approximately 4.2cm from the top of the Shrimp Member shales. A total of thirty-three squares were recorded at five levels within the 4.2cm thickness (Fig. 6.14).

Figure 6.14 Graph showing the distribution of all the faunal elements recorded within the 4.2cm thickness of Shrimp Member shale.



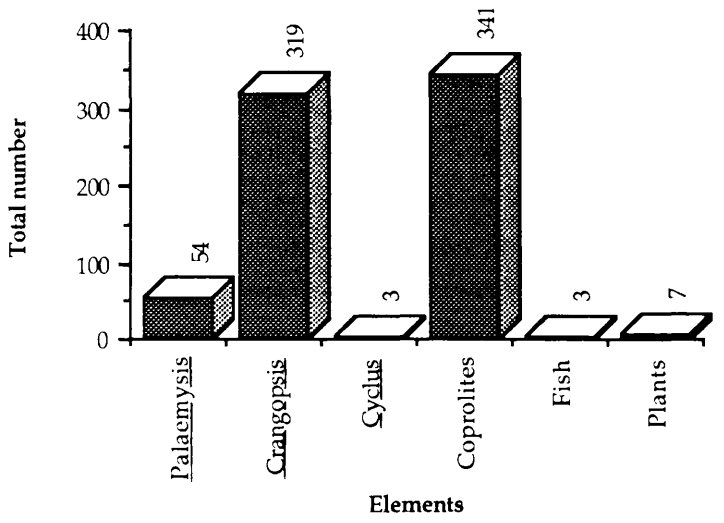
In general, the 'coprolites' (or enterospirae) seem to follow similar trends to *Palaemysis*. This suggests that the 'coprolites' were from animals which lived in similar environments to *Palaemysis*. *Crangopsis*, however, appears to have a negative correlation with *Palaemysis* indicating that their preferred life environment was different, although probably overlapped, which supports evidence provided by the cuticle chemistry (section 6.2.2), and the lateral distribution of *Crangopsis* and *Palaemysis* within the lagoon.

Figure 6.15 Diagram showing the relative proportion of the crustacean members of the fauna through the 4.2cm section of the Shrimp Member.



Since *Palaemysis* is thought to be a marine crustacean, the sharp increase in the proportion of *Palaemysis* relative to *Crangopsis* suggests that a minor marine influx occurred at 2.0cm, soon after a minor decrease in the marine signature (Fig. 6.15). The resolution of the analysis is approximately 0.5cm which is equivalent to approximately 50 laminations (=?50yrs). Even within the Shrimp Member it is, therefore, possible to demonstrate minor fluctuations in the salinity of the water influencing the environmental conditions of the lagoon.

Figure 6.16 Total number of fossils recorded from the excavation of the 33 square metres.



The comparatively large number of 'coprolites', collected from the Bearsden excavation, suggests that either there were a large number of fish present within the lagoon which were not preserved (Fig. 6.16), or that they floated into the lagoon. The total number of crustaceans recorded may be a factor of preservation potential of the crustaceans, and also, as a result of where the shales split. As the preservational conditions necessary for the preservation of 'coprolites' are different to those necessary for the preservation of the crustaceans, the total numbers cannot be used to demonstrate original proportions. The changes in the proportions of the different faunal elements, however, can be used to demonstrate environmental changes, such as is seen in the Shrimp Member above.

Plate 6.1

a) Spiral enterospire containing bivalves (HM NCA1; X3).

b) Spiral enterospire containing plant fragments (HM NCB2; X3.25)

c) Spiral enterospire containing only palaeoniscid fish fragments (HM NCD1; X4).

d) Collapsed spiral enterospire containing bivalves, acanthodian fish scales, and palaeoniscid fish scales (HM NCC1; X3).

e) Spiral enterospire showing convolute whorl structure and collapsed central portion. Contains mainly palaeoniscid fragments (HM NCC2; X3.25).

f) Structureless enterospire in phosphatic nodule as a result of internal collapse of the enterospire. Contains mainly palaeoniscid fragments (HM; X4). Irregular sedimentary structure to the laminations suggests shallow bioturbation.

g) Spiral enterospire containing palaeoniscid fragments and baryte pore filling cement (HM NCA2; X3).

h) Spiral enterospire containing abundant palaeoniscid fragments and kaolinite pore filling cement (HM NCB1; X3).

i) Spiral enterospire containing abundant bivalves and occasional fish fragment (HM; X3).

j) Small amphipolar coprolite, possibly from a crustacean (HM; X900).

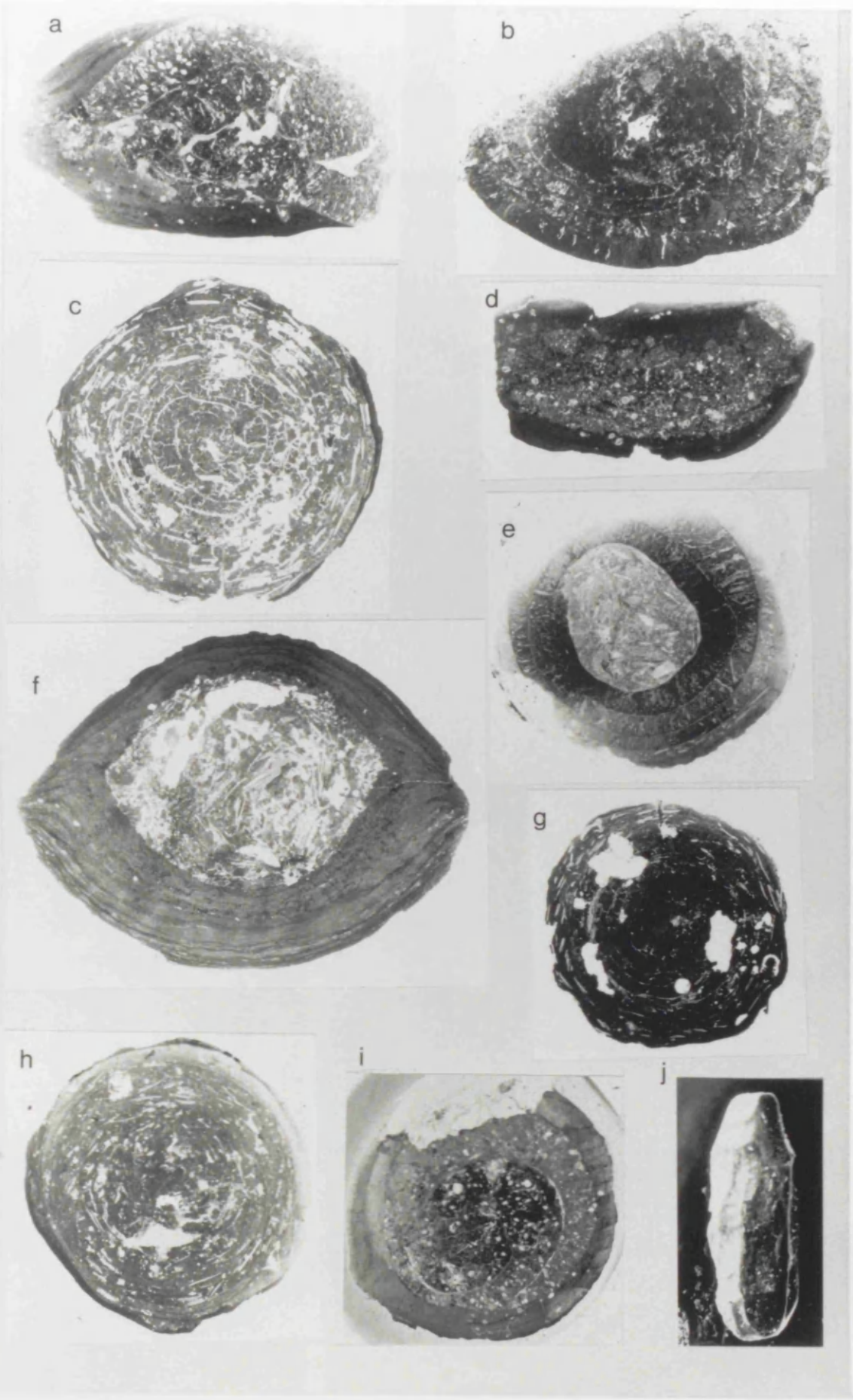
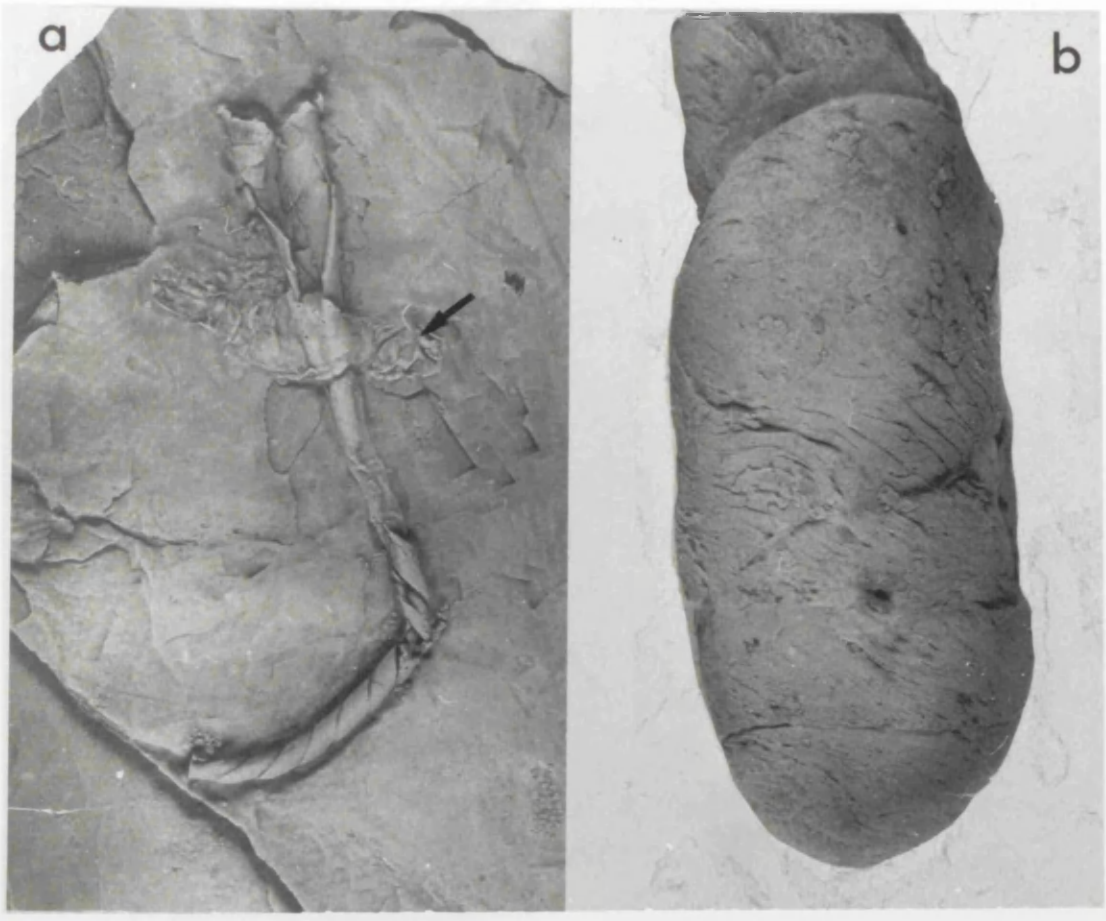

a
b
c
d
e
f
g
h
i
j

Plate 6.2

a) Distended heteropolar enterospire with *Crangopsis eskdalensis* (arrowed) (HM G642; X3).

b) Large compact heteropolar enterospire (HM; X1.85)


a
b

Chapter 7

Conclusions

The main purpose of this project was to produce a detailed study of the Carboniferous crustacean-bearing shale discovered at a locality in the Manse Burn, Bearsden, in 1981 by Mr. S. P. Wood. This locality, other localities discovered during the course of this study, and a number of previously recorded localities, containing shales at the same stratigraphical horizon and which contained fossil crustaceans, were placed in a stratigraphical, a palaeogeomorphological, and a sedimentological context. The diagenesis of the crustaceans was important in determining the early interactions taking place on the substrate surface. The palaeontology of the crustaceans was studied to provide a fuller understanding of their taxonomic position and functional morphology. As a result, it was possible to view these crustaceans in terms of their palaeoecological significance.

7.1 Stratigraphy.

The stratigraphical position of the shales was initially poorly constrained due to the lack of lithostratigraphical control at the type locality in the Manse Burn, Bearsden. The biostratigraphical position once determined, even in a broad sense, allowed other localities with shales of similar age to be traced, these latter, defined as representing part of the Manse Burn Formation, providing a more precise stratigraphical position for the shales.

The shales of the Manse Burn Formation contain conodont genera belonging to the *Kladognathus-Gnathodus girtyi simplex* Zone and spores of the *Bellispores nitidus-Reticulatisporites carnosus* (NC) Zone, both of which indicate a Namurian (Lower Carboniferous) age for this formation. This places the shales close to the lithostratigraphical horizon of the Top Hosie Limestone (THL). Goniatites, previously described by Currie (1954), from below

the THL, suggest that the THL is of the Pendleian E1 Zone.

The Manse Burn Formation was found to occur immediately above the THL at some localities, and lithostratigraphically, therefore, belongs to the Limestone Coal Group. The Manse Burn Formation has been subdivided into six members based on the sedimentological and palaeontological character of the shales; the Shrimp Member, the Posidonia Member, the Nodular Shale Member, the Platey Shale Member, the Betwixt Member, and the Lingula Member. The most important crustacean-bearing member of the formation being the Shrimp Member, which formed the basis of this project.

A number of localities were examined to determine the full extent of the Shrimp Member. The Shrimp Member was found to exist within the area confined to an area south of the Kilpatrick and Campsie Hills, and north of the Dusk Water, and East Kilbride. The Shrimp Member was not found west of Dalry, perhaps due to lack of exposure, but was not found on Arran where good exposures do exist at Laggan and Corrie. To the east, the Shrimp Member was not found further eastwards than the locality in the Corrie Burn, nor was it found at localities east of East Kilbride. At the localities, immediately surrounding this area, where the Shrimp Member was not developed, the THL was overlain by either a thick unfossiliferous micaceous shale (mostly in the east), or a thick sandstone unit.

The localities at which the Shrimp Member was found to be developed include:

1) Hindog Glen (NS27905115)

2) Swinlees Glen (NS29415342)

3) Powgree Burn (NS33635219)

4) Lochermill (NS24106472)

5) Bearsden (NS52947329)

6) Red Cleugh Burn (NS65567846)

7) Burniebrae Burn (NS66037818)

8) Corrie Burn (NS68707876)

9) East Kilbride (BGS bore hole data, filled quarries locations unknown).

7.2 Sedimentology.

Britain was situated in an embayment into the southern coast of the Laurasian continent close to the palaeoequator, during the Namurian (Lower Carboniferous). Several areas of positive relief which are contained within this embayment cause restricted access of marine waters into the Midland Valley of Scotland (MVS) at this time. The Scottish Carboniferous crustaceans, which are particularly well preserved in the low-energy environments which developed within this restricted area, may have acted as stock for the early dispersal of eumalacostracans (Schram *et al.* 1978). Many of these crustaceans are preserved in finely laminated sediments which were deposited in waters of variable salinity.

The Shrimp Member of the Manse Burn Formation in the MVS is a finely laminated shale deposited in a fault controlled basin, bound to the north by the Paisley Ruck and the Campsie Fault, and to the south by the Dusk Water Fault. The area between the Dusk Water Fault and the Inchgotrick Fault became an area of positive relief, soon after the deposition of the THL, forming a barrier to the more open marine waters to the south. At the same time, Arran also became a barrier to marine influence to the west.

The general mineralogical composition of the shales of the Shrimp Member is similar across the basin, suggesting that they were deposited under similar conditions. Throughout the Manse Burn Formation, the relative concentration of specific minerals varies significantly, especially with respect to pyrite. The more marine shales have a greater amount of pyrite due to increased sulphate reduction in the low-energy environment of the basin. The results suggest that the Posidonia Member and the Platey Shale Member are more marine in character than the Shrimp Member, the Nodular Shale Member, and the Lingula Member.

An analysis of the trace elements and rare earth elements further constrain the degree of marine water influence, and also the degree of oxygenation of the shales. The ratios of certain elements, such as Cr/V, Ce/Ce* and Th/U, and the

relative concentrations of others, such as Co, Ni, Rb, Sr, and Pb, indicates that;

1) the THL is an oxygenated marine deposit,

2) the Shrimp Member was probably deposited in a low oxygen environment with some marine influence,

3) the Posidonia Member is a marine deposit with variable oxygen levels,

4) the black mud from the Nodular Shale Member was a non-marine anoxic deposit, and,

5) the sediments were likely to have been derived from the erosion of a large continental area with significant input from the weathering of volcanic rocks.

The environment in which the shales of the Manse Burn Formation were deposited is generally a low-energy environment with variable oxygen levels, and salinity. The basin is restricted by structural controls as well as by river systems entering the MVS via the Kincardine Basin. The environment of deposition may be regarded as a back barrier lagoon which eventually silts-up towards the top of the Manse Burn Formation. The succession of sediments in the Manse Burn Formation broadly resembles that of a Yoredale cyclothem, with the THL at its base and the Kilsyth Coking Coal at the top.

7.3 Environmental controls on preservation within the Shrimp Member.

The fossils of the Shrimp Member have undergone a variety of taphonomic and diagenetic processes resulting in number of different styles of preservation. These forms of preservation can be grouped in terms of their mineralogy and mechanisms of formation. There are basically three mineralogical compositions, a francolitic, a pyritic, and a calcitic composition, with two mechanisms for the francolite formation, one for the pyrite, and three for the calcite.

The francolite can be formed either by the bacterial decay of soft body parts and gut fillings, in the case of the enterospirae, or by the buffered chemical

interaction of phosphate-rich waters with the calcareous shells of the crustaceans. The pyrite preserves some fossils by sulphate reduction and replacement of the calcareous shell in crustaceans and bivalves. The calcite preservation occurs either by the recrystallisation of the calcareous shell by bacterial degradation of the organic content (eumalacostracans and myodocopids), by the recrystallization of the aragonitic bivalve shells to form calcite, or by dissolution of calcareous shells and reprecipitation of drusy calcite in the resulting pore space (mostly eumalacostracans).

Phosphatisation is the best mode of preservation, resulting in much of the ultrastructural cuticular detail of the crustaceans being preserved. The mechanism by which the phosphatisation took place, and the chemistry of the francolite provides further constraints on the depositional environment of the Manse Burn Formation.

7.3.1 Mechanism of phosphatisation.

The phosphatisation of the amorphous carbonate cuticle of the Carboniferous crustaceans produces micronodular francolitic aggregates, amorphous phosphate, and hexagonally crystalline laths. It is likely that these structures result from chemical alteration of the cuticle rather than being directly induced by bacterial activity, as the phosphatisation prevents the normal chitinolytic decomposition of the crustacean cuticle. The higher-than-normal phosphate concentrations may have been derived from seasonal nutrient-rich fresh water input into the more marine waters of the back barrier lagoon causing algal blooms. On decomposition, the algae would release the phosphate concentrating it close to the substrate surface due to the low-energy of the environment. Phosphatisation of the crustaceans in the Shrimp Member, therefore, occurred in an anoxic low-energy restricted environment soon after a period of eutrophication.

The isotopic composition of the phosphates within an enterospire suggests both a marine source, based on the strontium ratio, and a meteoric source, for $\partial^{18}O$ and $\partial^{13}C$. This may indicate that the animal which produced the enterospire lived in the marine environment, but that the phosphatisation took place in a

non-marine environment. As phosphates concentrate strontium, and meteoric waters are generally depleted in strontium, it is likely that the strontium will reflect the original life-environment of the animal. The environment of phosphatisation of the enterospirae does not have to occur under the same environmental conditions as the phosphatisation of the crustaceans as there would be enough phosphate present within the enterospire to cause its own phosphatisation.

7.3.2 Constraints on francolite composition.

The chemistry of the francolite reflects either the chemistry of the waters in which the phosphate formed, or the original chemistry of the crustacean cuticle. The chemistry of the cuticle of the different crustaceans varies with respect to sodium and iron suggesting that either, the process of phosphatisation occurred in waters of differing composition, or that the crustaceans had different original cuticular compositions. The distribution of the crustaceans within the lagoon suggests that the crustaceans lived in waters of differing salinities and may have had different cuticular compositions to reflect this. The absolute concentrations of elements within the cuticle of the Carboniferous crustaceans is little different to those observed in the cuticle of extant crustaceans, and the process of phosphatisation does not appear to significantly influence the relative concentrations of the elements in the extant crustacean. This may be as a result of buffering solutions being produced within the cuticle during phosphatisation. The concentrations of the elements within the cuticle of the fossil crustaceans is, therefore, thought to reflect the original chemical composition of the crustaceans.

7.3.3 Diagenetic pore fluids within the Shrimp Member.

The enterospirae provide a unique opportunity to determine the diagenetic history of the shale. Pore spaces are provided by secondary tension gaps, and by some original pores within fish teeth and bivalves. After consolidation of the enterospirae, several pore-cements can be recognised which are unrelated to the decomposition of the enterospire. These consist mainly of calcite, quartz, and kaolinite cements, although there is also a late baryte cement in some samples. The absolute timing of the different diagenetic events is difficult to assess,

although it is thought that the final kaolinite cementation was soon after the formation of the nodules. The baryte cement occurred after this, perhaps relating to some fault related pore-fluid migration, deriving from the surrounding volcanic rocks.

7.4 Carboniferous crustaceans from the Manse Burn Formation.

Five eumalacostracan genera were obtained from the Manse Burn Formation, including, *Tyrannophontes pattoni*, *Tealliocaris robusta*, *Crangopsis eskdalensis*, *Palaemysis dunlopi*, and *Minicaris brandi*, and one copepod, *Cyclus rankini*. None of these species are new, although their taxonomic positions and nomenclature are controversial. On the basis of a cladistic analysis on preservable morphological features, it was concluded that many of the fossil genera could be placed in extant groupings. *Minicaris* could be placed with the Syncarida, *Tealliocaris* with the Decapoda, and *Tyrannophontes* with the Stomatopoda. *Crangopsis* and *Palaemysis*, however, could not be placed in any extant group with confidence, as the Mysida and the Euphausiacea were difficult to distinguish between using this method. It was adjudged necessary to place these fossils together in a single crown group, the Eocarida. *Cyclus* was found to be more similar to the copepods than to the branchiopods using a similar morphological method.

7.4.1 Morphology and affinities of the crustaceans from the Manse Burn Formation.

More specimens of *Tyrannophontes pattoni* are now available than were when Schram (1979) first suggested that *Perimecturus pattoni* could be a representative of the tyrannophontids. New evidence on the nature of the tail fan confirms Schram's hypothesis allowing this species to be placed with the tyrannophontids.

Newly observed similarities between the Scottish specimens of the genera *Tealliocaris* and *Pseudotealliocaris*, such as the large third abdominal somite, the lateral expansion of the second abdominal somite, the oval processes on the second and third abdominal somites, and the three marked

ridges projecting through the arthrodial membrane, indicate that these two genera are congeneric. The specimens of the different species of *Tealliocaris* also have similar morphometric ratios with regards to the width and length of the telson, and the lengths of the abdomen and carapace. Three species of Scottish tealliocarids are recognised as a result of this study, *T. woodwardi*, *T. etheridgii*, and *T. robusta*, differentiated on the basis of the number of spines on the antennal scales, the ornamentation of the keels, and the presence of transverse grooves on the abdominal tergites.

Specimens of *Crangopsis* from the Manse Burn Formation are similar in form, and dimensions, to *Crangopsis eskdalensis* from Glencartholm, in the Northumberland Trough area. Newly observed structures include the presence of at least four thoracic somites free of the carapace, and the presence of a possible sensory devise on the second abdominal somite. A comparative study of *Waterstonella*, from Granton, near Edinburgh, and *Crangopsis* from the same locality suggests that these two crustaceans are congeneric, and belong to the species *C. socialis*. The differences, initially thought to be generic, between these two morphologies are a result of preservational factors, and a full range of morphologies between the two end member morphologies can be observed.

Palaemysis differs substantially from *Anthracophausia* despite having been considered synonymous by Brooks (1969). The differences include the presence of a large rostrum in *Anthracophausia*, the shape of the telson and uropods, the shape of the abdominal pleura, and the presence of a large pair of anterior spinose appendages in *Palaemysis*. *Aratidecthes* may also represent a species of *Palaemysis*, as it has a similar general morphology and identical tail fan. Only one species of *Palaemysis* could be recognised as the species were first erected on the basis of poorly preserved tail fans (Peach 1908) which could not be adequately differentiated between morphometrically or morphologically. The species of *Palaemysis* is therefore taken to be that of the original type species, *P. dunlopi*.

Minicaris brandi was described from poorly preserved specimens in a bore-hole sample (Schram 1979). The similarity between the tail fan of the type

specimen and the tail fans of specimens from the Manse Burn Formation indicates that these specimens are congeneric. New features of this crustacean, which include the biramous annulate and setiferous pleopods, the shape of the cephalic shield, the ornamentation of the thoracic and abdominal tergites, suggest an affinity with the genus *Squillites*.

The morphology and relative dimensions of *Cyclus rankini* indicates that the two forms of *Cyclus*, the flat forms and the convex forms, result from differences in the preservational environment rather than from taxonomic differences. The number, and relative position, of the sectors, or tergites, of the thorax are identical for the two forms. New features of the morphology of *C. rankini*, such as the abdomen, the sexual appendages, the ventral morphology, and the number of limbs, suggest an affinity with extant copepods. The morphology of *C. rankini*, and its association with byssate bivalves, further suggests that this animal lived amongst seaweed. Its presence in a variety of preservational environments can be explained by being carried by the algae into these different environments.

7.4.2 Cuticular structure.

The ultrastructure of the cuticle of *Tealliocaris* from the Manse Burn Formation is similar to that found in extant crustaceans. A study of thin sections and broken sections of the exocuticle, suggests that the cuticle is composed of helicoidally arranged pore canals, interrupted by straight tegumental ducts which traverse the cuticle. This is the first record of such structures in fossil crustaceans, although other workers have inferred these structures to exist in Jurassic and Cretaceous decapods.

Three divisions of the cuticle can be recognised, the epicuticle, the exocuticle, and the endocuticle which is separated from the exocuticle by the line of emergence.

The surface structure of the epicuticle of *Cyclus* is different to the surface of the epicuticle of the other crustaceans in that it is composed of fine thread-like

corrugations. This is similar to structures described to exist on extant copepods.

7.5 Palaeoecology of Carboniferous crustaceans from the Manse Burn formation.

Tyrannophontes pattoni, *Tealliocaris robusta*, *Crangopsis eskdalensis*, *Palaemysis dunlopi*, and *Cyclus rankini* were all present in the environment during the period at which phosphatisation took place. *Minicaris brandi* is preserved differently from the other crustaceans and is not thought to have been present in the environment at the same time as the other phosphatised crustaceans. The phosphatised crustaceans are thought to have interacted as a community, the Western Midland Valley of Scotland Crustacean Palaeocommunity.

The major control on the distribution of the crustaceans within the same basin is likely to be salinity. Temperature would not vary much in the equatorial region, the sedimentation rate is the same across the basin, and the water depth and oxygenation levels also do not appear to have been significant factors as the character of the sediment in the Shrimp Member does not change much across the lagoon.

The diversity and concentration of crustaceans varies across the lagoon from a locality containing only *Crangopsis*, in the west, through localities containing *Crangopsis* and *Palaemysis*, to localities with the full complement of crustacean genera in the east. The abundance of crustaceans also appears to increase from west to east.

The chemistry of the cuticle of these crustaceans also appears to complement this adaptation to different salinities. The higher the sodium concentration in the cuticle, the closer to the mouth of the lagoon are the crustacean genera. The chemistry of the cuticle of the crustacean may reflect the chemistry of the environment in which the cuticle formed, as does the blood of extant crustaceans (Lockwood 1968). The relative sodium enrichment of the cuticle of *Tealliocaris* relative to *Crangopsis*, *Tyrannophontes*, and *Palaemysis* coupled with the

abundance of *Tealliocaris* in hypersaline environments, suggests that it was a euryhaline osmo- hyporegulator.

The abundance of *Crangopsis* in most environments, except freshwater and hypersaline environments, the abundance of tegumental ducts, and the low sodium content of the cuticle suggests that it was a euryhaline osmoconformer relative to *Tealliocaris*.

Palaemysis and *Crangopsis* frequently occur together in a more brackish water environment within the lagoon, although *Palaemysis* does not extend over the full range of conditions tolerated by *Crangopsis* to the west. *Tyrannophontes*, however, is very restricted in its environmental tolerance and is found only in the eastern-most localities of the lagoon. The sodium concentrations of the cuticle indicate that *Crangopsis* produced its cuticle in less marine environments than *Palaemysis* and *Tyrannophontes*, and that *Tealliocaris* produced its cuticle in an environment of higher salinity. *Tyrannophontes* is likely to have been stenohaline and adapted to near normal marine salinities, whereas, *Palaemysis* was more euryhaline and possibly an osmoconformer. No firm conclusions can be drawn from this evidence, however, as only a few data points exist at the moment. Further work on the chemistry of the cuticle as well as the isotope geochemistry of extant and fossil crustaceans may support the above view. The evidence presented can only suggest a correlation between the sodium concentration of the cuticle of the fossil crustaceans and the environmental salinity conditions.

7.6 General overall statement.

The results of this study show that Carboniferous crustaceans can be used as sensitive environmental indicators of salinity conditions. Their mode of preservation can also help in determining rapid changes in environmental conditions. The distribution of these crustaceans within a single horizon over a single basin can give an indication of the salinity gradients, and therefore, the source direction of marine and non-marine waters.

The morphology and taxonomy of these crustaceans indicate that, despite the apparent rapid diversification towards the end of the Devonian, eumalacostracan crustaceans have not evolved greatly through time, and that many extant orders are represented at an early stage in their development.

The application of community evolution to crustacean palaeocommunities is made difficult due to their poor preservation potential.

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APPENDIX

Vanadium analyses by spectoscopic determination

INTRODUCTION: Vanadium forms a yellow complex with alkali tungstate in solutions containing phosphoric acid. The vanadium is concentrated as a complex with 8-hydroxyquinoline.

REAGENTS:

a)	8-HYDROXYQUINOLINE SOLUTION:	dissolve 1gm in 100ml of 2N acetic acid (116ml concentrated acid in 1000ml water)
b)	CHLOROFORM:	
c)	SULPHURIC ACID 6N:	add 162ml concentrated acid to 800ml water in a 1000 ml measuring cylinder. Allow to cool and add water to the mark.
d)	PHOSPHORIC ACID 5N:	105ml concentrated acid in water and dilute to 1000ml
e)	SODIUM TUNGSTATE SOLUTION:	dissolve 8.25gms of the dihydrate in 50ml water.
f)	STANDARD VANADIUM SOLUTION (STOCK):	dissolve 0.230gms of dried ammonium metavanadate in water and dilute to 500ml with water (contains 200gms/ml V).
g)	STANDARD VANADIUM WORKING SOLUTION:	dilute the stock solution with water to give a working standard containing 10ugms/ml V (5.0ml stock solution diluted to 100ml).
h)	2% SODIUM CARBONATE SOLUTION:	dissolve 20gms anhydrous sodium carbonate in water and dilute to 1000ml.
i)	ANHYDROUS SODIUM CARBONATE:	
j)	POTASSIUM NITRATE:	

k) METHYL ORANGE INDICATOR SOLUTION: dissolve 0.05gms solid in 100ml water.

PROCEDURE: Accurately weigh 0.5 gms of finely powdered sediment in a platinum crucible, add 3gms anhydrous sodium carbonate and 0.1gms potassium nitrate. Fuse the mixture over a meker burner for 30 minutes.

Extract the melt with hot de-ionised water (approximately 90°Celsius), vacuum filter using a medium or close-textured paper (Whatman No. 40 or 42) and wash well hot 2% sodium carbonate solution. Discard the residue and combine the filtrate and washings. Dilute in de-ionised water to a concentration within the range 1-6ppm if necessary.

Transfer the solution to a 100ml separating funnel, add 4 drops of methyl orange indicator solution and titrate with 6N sulphuric acid until the indicator turns pink. Swirl the solution to get rid of as much carbon dioxide and add 1ml of 8-hydroxyquinoline solution and 3ml of chloroform. Shake the solution for 1-2 minutes to extract the dark coloured vanadium complex, allow the phases to separate and remove the chloroform layer to a platinum crucible. Rinse the funnel with a little chloroform. Add a further 0.5ml of 8-hydroxyquinoline solution with 3ml of chloroform and again extract by shaking for 1 minute. If the extract shows an appreciable dark colour repeat the extraction for a third time etc. discard the aqueous solution.

Add 0.1gms of sodium carbonate to the chloroform extracts (in the platinum crucible) and allow the chloroform to evaporate. Burn off the organic matter and fuse the residue to convert all the vanadium to sodium vanadate. Dissolve the melt by warming with 2-3ml of water, add 1ml of 6N sulphuric acid, 1ml of 5N phosphoric acid and 0.5ml of sodium tungstate solution. Heat to boiling, cool, transfer to a 10ml volumetric flask and dilute to the mark with water. Measure the optical density relative to water in 1cm cells using ultraviolet/visible spectrophotometer set at 400nm. Prepare a blank solution using the same method as before but omitting the rock powder.

Vanadium concentrations (ppm):

Top Hosie Limestone	11.45
Shrimp Member	50.7
	53.9
Posidonia Member	45.3
	41.9
Nodular Shale Member	57.8
	53.55

CALIBRATION: Transfer aliquots of 1-6ml of the standard vanadium working solution to separate 10ml volumetric flasks and add to each:

1ml 6N sulphuric acid

1ml 5N phosphoric acid

and 0.5ml sodium tungstate solution

Also prepared a standard blank with no standard vanadium working solution and all the above reageants. This gives standards containing:-

1ugm/ml V

2ugm/ml V

3ugm/ml V

4ugm/ml V

5ugm/ml V

6ugm/ml V

Plot optical density (abs) versus concentration for the corrected standards annd read off the unknown concentrations from the corrected optical densities. These are then calculated up depending on the dilution prior to the extraction.

Spores

Acanthotriletes =Acan.; Anapiculatisporites = Anap. ; Auroraspora = Auror.; Bellispores = Bell.; Calamospora = Cala., Calam.; Cingulizonates = Cing.; Convolutispora = Conv.; Crassispora = Crass.; Densosporites = Denso.; Dictyotriletes = Dict.; Granulatisporites = Granu.; Grumosporites = Grumi.; Knoxisporites = Knox.; Leiotriletes = Leio.; Lycospora = Lyc.; Microreticulatisporites = Micro.; Procoronaspora = Proc.; Punctatisporites = Punct.; Savitrisporites = Sav.; Shulzospora = Schulz.; Tholisporites = Thol.; Tripartites = Trip.; Verrucosisporites = Verr.; Waltzispora = Waltz.

NSM = Nodular Shale Member; THL = Top Hosie Limestone; SM = Shrimp Member.

Spores

	Spore name	black mud (NSM)	THL	SM
1	Lycospora	386	305	351
2	Densospora	33	93	93
3	Leiotriletes	34	58	32
4	Neoraistrichia	10	6	7
5	Schulzospora	10	2	16
6	Tripartites	14	15	10
7	Triquitrites	5	1	4
8	Triquitrites (spiney)	1		1
9	Punctatisporites	32	24	20
10	Convolutosporites	13	14	6
11	Knoxisporites	6	2	12
12	Florinites	3	52	
13	Camptotriletes	1		
14	Anapiculatisporites	1		
15	thin Triquitrites	1		
16	Cingulozonates		1	
17	X J150		6	
18	E500		2	

spores A

	spore	NC7	NC5	NC7
1	Acan.falc	0	1	1
2	Anap. min	1	0	1
3	Auror.sol	1	0	1
4	Bell.nitid	2	1	3
5	Cala. brev	2	0	2
6	Cala. micro	3	0	3
7	Calam.mac	0	1	1
8	Cing. cap	3	0	3
9	Cing.bial	2	0	2
10	Conv.var	0	2	2
11	Crass. mac	2	0	2
12	Denso. inter	8	14	22
13	Denso. spin	1	0	1
14	Denso. trian	7	5	12
15	Denso.annu	9	9	18
16	Dict.cast	1	2	3
17	Granu.granu	0	1	1
18	Granu.piri	3	0	3
19	Granu.pol	0	11	11
20	Grumi. inae	4	1	5
21	Grumi.rufus	0	1	1
22	Knox.cint	0	7	7
23	Leio. pr	9	3	12
24	Leio.sp	0	1	1
25	Lyc. p	44	28	72
26	Lyc.noc	84	84	168
27	Lyco.rug	1	0	1
28	Micro.punct	3	0	3
29	Proc.amb	0	1	1
30	Punct.aer	0	2	2
31	Punct.min	1	5	6
32	Punct.nit	0	1	1
33	Punct.sp	0	1	1
34	Sav.nux	0	1	1
35	Schulz.elon	9	15	24
36	Thol.scot	0	1	1
37	Trip.simp	2	0	2
38	Trip.tril	3	3	6
39	Verr.cer	1	0	1
40	Waltz. pol	3	2	5

Crustacean Data.

a) *Tealliocaris*; dimensions. wt = width of telson; lt = length of telson; la = length of abdomen; lc = length of carapace; lr = length of rostrum; ls = length of antennal scale; Tl = total length; ant. spines = number of spines on the antennal scale (measurements in mm).

b) *Crangopsis*; dimensions. ls = length of antennal scale; lc = length of carapace; la = length of abdomen; l6 = length of sixth abdominal somite; luex = length of uropodal exopod; C = *Crangopsis* from Granton; B = *Crangopsis* from Bearsden; W = *Waterstonella* from Granton (measurements in mm).

c) *Palaemysis*; dimensions. lt = length of telson; luex = length of uropodal exopod; l6 = length of sixth abdominal somite; ls = length of antennal scale; la = length of abdomen; lc = length of carapace; 1 = *Palaemysis* from Bearsden; 2 = *Palaemysis* from Granton; BGS = *Anthracophausia* held by the BGS Edinburgh; Notts = *Anthracophausia* held by the BGS Nottingham; EK = *Palaemysis* from East Kilbride; SH = *Palaemysis* from the Red Cleugh Burn, Spouthead (measurements in mm).

d)*Tealliocaris*; tegumental ducts. lc = length of carapace; p/c = number of tegumental ducts along length of carapace; Gull (G) = Gullane; B'den (B) = Bearsden; Duns (D) = Duns; Glen (GL) = Glencartholm (measurements in mm).

e) *Cyclus*; dimensions (measurements in cm).

f) *Tealliocaris*; cuticular chemistry.

g) Cladistic matrices of fossil and Recent Crustacea.

h) XRD-trace of the francolite in the cuticle of *Palaemysis*. P = Francolite peaks; Q = quartz peaks; K = clay peaks.

i) Probe analyses of fossil and Recent Crustacea. T = *Tealliocaris*; P = *Palaemysis*; B = *Tyrranophontes*; C = *Crangopsis*; SED = sediment; CN = phosphatic nodules; MC = *Cancer* (MC8-12 after phosphate treatment).

a

Glasgow	wt(1)	lt(1)	la(1)	lc(1)	lr(1)	ls(1)	Tl(1)	ant.spines
G40	3.40	4.90	12.00	11.30	7.20	5.10	29.10	6.00
G43	2.50	3.80	8.40	10.90	6.10	4.10	24.60	6.00
G51	3.00	5.00	10.30	13.00	7.10	4.50	31.00	6.00
G52	3.60	5.80	13.50	14.60			31.40	6.00
G53	2.80	5.30	9.50	9.40	5.00	5.20	29.30	6.00
G55	2.90	4.40	10.20	12.00	7.10	5.00	28.70	6.00
G63		3.20	6.70	7.60	3.90	3.70	18.50	7.00
E.SPEC	3.00		8.20	11.00	6.50	4.90		
G500	3.40	5.40	12.00	13.90	4.90	6.90	32.60	
1887.25.1035	1.50	2.90		6.00	3.00		15.50	
1887.25.1036	2.00	2.70						
1887.25.1034				17.00				
1887.25.1033				15.00	6.50			

Grant+Glenc	wt(3)	lt(3)	la(3)	lc(3)	lr(3)	ls(3)	Tl(3)	ant.spines
Gr1	3.60	4.40	11.30	12.00	4.40	5.00	28.80	
Gr2			13.70	15.50	7.70	5.50	35.60	>6
Gr3		6.90	18.00	21.00	5.50	6.50	48.00	>7
1881.39.4	3.30	4.70	10.90	15.00	6.50	4.90	31.80	8
1957.1.5014				9.90	4.10			9
1958.1.2652	3.40	4.50	10.60	13.60	6.30	4.90	31.00	9
5915	2.00	2.50	3.90	6.40			15.20	8
5918	5.10	5.50	15.00	14.70	7.20	7.20	39.90	
5919	5.40	7.00	16.50	18.40	12.20	7.50	50.80	
5920				16.00	5.50	6.80		
5922	4.00	6.00	10.00	12.50	8.50	5.00	30.00	
5925	1.30	1.80	3.40	5.00	2.30		11.00	
5926	1.30	1.50	3.40	4.00	1.80	1.80	9.60	
5928	2.40	4.50	9.50	11.30			22.10	
5929	3.90	6.80						
5921				13.80	8.40			
I9281(1)	4.30	5.40	15.30	14.80	5.80		27.60	
I9281(2)	3.00	3.70	10.00	11.00			23.40	
13470	3.00	5.50	10.50	13.50	4.60	5.90	31.60	
13471	3.70	5.20	11.10	14.20	5.00	7.00	34.60	
13472	3.50	4.50	9.00	12.10	3.70	4.00	26.90	
13473	4.00	6.10	13.00	16.00			34.90	
13474	3.70	5.00	13.00	14.90			33.70	
13475	2.20	3.30	5.80	7.40			17.10	
13477	2.80	3.80	9.90					
In35334	3.50	4.00	10.00	11.50	3.30		25.90	
35335	4.20	6.80	10.90	17.00			41.60	
35338	3.40	4.90	8.90	12.70	4.20	7.00	30.70	
35353	3.10	4.90	14.40	12.90			27.30	
38016	3.50	4.20	11.80	13.30			29.50	
38022	5.20	6.80	18.80	20.90	7.40		48.80	
60057	4.50	7.10	18.00					
60060	4.40	5.20	13.00					
60092	4.90	6.40	12.60	19.00	4.50		41.40	
60094				17.60	5.20			
60095	5.20	6.40	13.10	15.00	4.60		38.30	
60108	3.50	4.50	11.90	15.00	3.20	5.60	31.20	
I891	2.00	2.60	7.40	8.00	2.80	4.30	18.60	
I7265								
1887.25.1035	1.50	2.90		6.00	3.00		15.50	
1887.25.1036	2.00	2.70						
1887.25.1034				17.00				
1887.25.1033				15.00	6.50			

Gullane	wt(2)	lt(2)	la(2)	lc(2)	lr(2)	ls(2)	Tl(2)	ant.spines
1	1.90	2.30	6.40	8.90		3.00	19.20	
2	2.30	3.10	8.60	9.00		3.10	20.50	2.00
3	1.50	2.90	6.50	7.40		2.10	18.50	2.00
4		4.10	8.70	11.90		3.20	21.40	2.00
A1965	3.10	4.50	10.40	12.30			29.30	3.00
G432	2.70	4.50	10.50	13.80	4.60	6.90	30.30	4.00
G313	3.00	4.20	11.30	12.40	4.20	7.80	32.20	4.00
G465	0.50	0.70	2.60	3.00		1.30	7.50	4.00
G434	1.90	2.90	6.00	9.20	3.50	4.30	20.00	4.00
G433	2.60	4.50	11.50	14.40	4.30	5.90	29.00	3.00
G327	3.20	5.00	11.80	14.50	3.80	7.30	32.70	2.00
1974.42.24	1.70	3.40	10.90	11.40	3.80	4.90	28.50	4.00
1974.42.84	2.00	4.20	10.40	13.20	4.40	5.50	30.70	3.00
1974.42.31	2.80	4.50	9.60	14.50	4.20	6.40	33.40	3.00
1983.18.11	2.30	3.90	8.50	12.10	3.40	5.10	26.00	3.00
1974.42.23	4.00	5.30	14.20	15.50		8.90		3.00
A2252	4.60	5.00	12.50	12.80	8.00	5.20	24.50	2.00
								9.00

b

Crang/Water data

no.	ls	lc	la	16	luex	ls(C)	lc(C)	la(C)	16(C)	luex(C)	ls(B)	lc(B)	la(B)
1		3.70	5.80	2.30	2.50							5.00	7.50
2		4.70	7.70	3.50								4.00	9.30
3		3.00	4.60	1.90								5.40	11.20
4		3.00	7.10	2.40								5.70	10.50
5		3.10	6.20	2.60								3.90	8.20
6	0.90	3.40	5.50	2.50	2.90						1.90	3.70	8.20
7	1.10	3.20	5.10	2.00	2.50						1.10	4.10	7.30
8	1.10	3.60	7.50	2.90							1.10	6.00	10.80
9	1.15	3.20	6.30	2.00							1.50	5.10	10.90
10	1.15	3.50	5.00	2.40	2.10						1.50	5.60	9.20
11	1.30	4.00	7.30	2.50								3.00	6.40
12	1.40	4.90	6.70	2.70								3.70	8.50
13	1.50	4.30	6.30	2.80								4.50	9.00
14	1.60	4.20	7.60	3.20	3.10							6.40	10.00
15	1.60	4.80	7.30	3.00	3.30						2.20	4.80	8.00
16	1.70	4.70	8.20	3.20	3.60	2.70	7.50	15.20	5.90	5.40	2.20	4.60	9.60
17	1.80	3.80	9.10	2.80		3.00	8.50	15.10	5.30				
18	1.80	3.35	5.70	2.20	3.00	3.20	9.10	17.10	5.40				
19	1.90	3.60	6.00	2.30	3.00	10.40	31.70	52.70	18.00				
20	2.00	4.80	7.10	2.50	3.30	10.50	31.70	48.70	19.60				
21	2.00	4.10	8.10	2.90		8.10	25.70	51.70	16.70				
22	2.10	5.30	10.00	3.30	3.40		25.50	46.90	16.50				
23	2.20	6.80	10.70	3.20									
24	2.40	5.60	8.40	2.70									
25	2.60	6.40	9.80	3.20									
26	14.50	22.00	49.55	16.60	21.60								

A7

Crang/Water data

	16(B)	ls/lc	ls/16	lc/la	16/lc	ls/lc(C)	ls/16(C)	lc/la(C)	16/lc(C)	ls/lc(B)	ls/16(B)	lc/la(B)	16/lc(B)
1	3.50			0.64	0.62							0.67	0.70
2	2.90			0.61	0.74							0.43	0.72
3	3.60			0.65	0.63							0.48	0.67
4	3.00			0.42	0.80							0.54	0.53
5	2.20			0.50	0.84							0.48	0.56
6	2.20	0.27	0.36	0.62	0.73					0.51	0.86	0.45	0.59
7	1.90	0.34	0.55	0.63	0.62					0.27	0.58	0.56	0.46
8	3.40	0.31	0.38	0.48	0.81					0.18	0.32	0.56	0.57
9	2.90	0.36	0.57	0.51	0.62					0.29	0.52	0.47	0.57
10	2.90	0.33	0.48	0.70	0.69					0.27	0.52	0.61	0.52
11	1.70	0.33	0.52	0.55	0.62							0.47	0.57
12	2.50	0.29	0.52	0.73	0.55							0.43	0.68
13	2.60	0.35	0.54	0.68	0.65							0.50	0.58
14	3.10	0.38	0.50	0.55	0.76							0.64	0.48
15	2.30	0.33	0.53	0.66	0.62					0.46	0.96	0.60	0.48
16	3.50	0.36	0.53	0.57	0.68	0.36	0.46	0.49	0.43	0.48	0.63	0.48	0.76
17		0.47	0.64	0.42	0.74	0.35	0.57	0.56	0.33				
18		0.54	0.82	0.59	0.66	0.35	0.59	0.53	0.24				
19		0.53	0.83	0.63	0.64								
20		0.42	0.80	0.68	0.52								
21		0.49	0.69	0.51	0.71								
22		0.40	0.64	0.53	0.62								
23		0.32	0.69	0.64	0.47								
24		0.43	0.89	0.67	0.48								
25		0.41	0.81	0.65	0.50								
26													

Crang/Water data

	ls(V)	lc(V)	la(V)	16(V)	luex(V)	Schram '79	lc	la	16
1	7.10	20.90	31.00	12.20	15.80	GSE 5007	8.00	19.80	7.00
2	7.00	19.90	30.00	9.90	16.40	GSE 5841		20.00	5.00
3	6.00	14.70	28.20	11.60	15.30	GSE 5844	8.20	22.50	5.20
4	8.70	20.20	33.60	12.00	16.00	GSE 5846	7.00	17.20	
5	8.40	22.00	32.80	-11.10	16.20	R 1957.1.5110	7.70	19.50	
6	9.60	28.70	42.90	13.80	22.50	E 13497	9.60	25.50	
7						1524	6.00	15.00	
8									
9									
10									
11									
12									
13									
14									
15									
16									
17									
18									
19									
20									
21									
22									
23									
24									
25									
26									

C

PALAMYSIS DATA

	lt(1)	luex(1)	l6(1)	ls(1)	la(1)	lc(1)	lt(2)	luex(2)	l6(2)	ls(2)	lt(BOS)	l6(BOS)	luex(BOS)	la(BOS)	lc(BOS)	lt(GG)	l6(GG)	luex(GG)	lt(Notts)	luex(Notts)	l6(Notts)	lt(EE)	luex(EE)
1	9.4	13.5	8.0	11.0			7.6	11.5	8.5	11.0	4.5	6.0	6.4	20.5		5.5	7.0	7.3	5.8	9.0		6.4	7.5
2	10.9	15.1	8.2	10.5			8.6	13.0	9.3		5.0	7.0	7.3			6.4	5.0	8.0	8.3	10.5	6.5	8.0	16.5
3	7.4	13.1	7.5				7.8	12.5	8.8	11.0	5.4		7.3						5.7	7.4	5.5		
4	8.5	11.5	10.5				10.5	14.5	11.9		4.5	7.1		23.0	14.5				4.5	7.0	4.6		
5	6.6	11.2	6.0	9.0	30.0	15.9	11.5	15.0	14.0		6.6	5.4		21.0	11.3								
6	10.0	15.5	10.0	11.2			5.9	8.1	6.1		3.5	3.8	4.2										
7	5.7	9.4	5.8		25.7		10.6	14.2	11.4	12.5	5.0	6.3		21.0	13.0								
8	9.2	12.4	7.9					12.7	10.0														
9	9.4	13.9	8.5				9.0	12.5	10.0														
10	8.9	12.9	8.1				6.3	10.7	9.0														
11	9.8	14.4	8.4				5.5	8.9	6.5														
12	10.0	13.7	7.5		42.5	19.9	10.5	14.5															
13	8.5	11.5	10.5	8.6	27.5	16.4	7.7	12.0	9.0	9.9													
14	9.1	14.0	7.1																				
15	7.8	11.4	6.9																				
16	7.0	11.9	7.9																				
17	8.9	11.9	7.3																				
18	8.1	14.5	9.0																				
19	7.5	12.3	6.5																				
20	8.9	13.0																					
21	9.0	14.2	8.0	10.0																			
22	10.0	15.6	9.0																				
23	8.9	12.6	7.5																				
24	10.9	14.2	8.4																				
25	8.5	14.1	9.9	9.8																			
26	10.2	15.0	10.0	10.9	46.8	15.1																	
27	8.5	13.2	7.9	9.4	35.5	17.0																	
28	10.5	16.7	9.8																				
29	8.1	13.8	6.5																				
30	8.5	14.0	10.0	10.5																			
31	8.3	11.6	8.1	10.4																			
32	8.8	13.5	7.3	11.9																			
33	8.5	12.2	7.3																				
34	9.8	14.2	10.5																				
35	9.1	13.3	11.1																				
36	8.8	14.2	9.3	11.0																			
37	6.0	12.0	10.1																				
38	10.2	15.0	11.9	8.1	43.1	13.2																	
39	8.9	15.0	8.1	9.1																			
40	10.3	14.2	10.0	10.5	33.0	12.4																	
41	6.8	11.1	7.0		37.0	17.8																	
42	9.5		9.8	9.4																			
43	9.3	14.9	9.6																				
44	7.5	14.6	8.1	12.2																			
45		12.3	8.9																				
46			9.5		38.5	16.0																	
47			8.2		27.7	13.9																	
48	7.8	12.0	7.3	9.9	30.5	14.0																	
49	8.1	11.0																					
50	5.8	7.6	4.6																				

PALAMYSIS DATA

	l6(EE)	la(EE)	lc(EE)	ls(EE)	T1(EE)	lt(SH)	luex(SH)	l6(SH)
1	5.0	15.9	13.5	5.0	36.0	8.1	12.9	10.5
2	13.4					9.0	11.9	
3						8.4	11.9	11.4
4						7.2	10.0	8.0
5						6.9	10.3	9.0
6						7.0	10.4	7.6
7						7.5	11.5	
8						6.4	8.1	6.8
9						6.9	8.1	7.9
10						6.5	8.9	
11						8.3	10.4	8.5
12						8.0	11.7	
13								

d

PITS Tealliocaris

	pits/mm2	Ic	Spec (GULL)	pits/mm2	Ic	B'den	p/c,G	p/c,B
1	144	8.7	GY1957.1.5036	43	13.9	G500	1252.8	597.7
2	144	7.5	GY1983.18.3	47	11.3	G40	1080.0	531.1
3	130	7.8	GY1967.1.5062	44	13.0	G51	1014.0	572.0
4	100	14.5		57	9.4	G53	1450.0	535.8
5	81	20.0		45	12.0	G55		540.0
6				77	7.6	G63		585.2

PITS Tealliocaris

	pits/mm2	Ic	spec (DUNS)	p/c,D	pits/mm2	Ic	spec (GLEN)	p/c,GL
1	36	13.33	BGS5942	479.88	44	8.6	BGS5916	344

e

CYCLUS DATA

	C. rankini	Fulllength	Width of thorax	Length of thorax	C. martinensis	Fulllength	Length of thorax	Width of thorax
1	1	1.170	0.900	0.500	GSM102638	1.250	0.667	0.967
2	46	0.730	0.560	0.370	102639			
3	A2803/3	1.260			102640	1.117	0.700	0.883
4	A2806/2	0.830	0.590	0.370	102642	1.150	0.717	0.883
5	105		1.100	0.790	102643a	0.883	0.567	0.700
6	106		0.910	0.610	102643b	0.933	0.583	0.700
7	A2803/2		1.200	0.820	102644	1.267	0.783	0.950
8	A2806/1		0.400	0.340	102645	0.967	0.617	0.700
9	A2807	1.160	0.870	0.570	102646	0.900	0.583	0.667
10	A2806/3	1.150	0.960	0.610	102647	1.300	0.833	0.967
11	A2803/1	1.600	1.000	0.780	103068	1.183	0.800	1.033
12	G64	1.400	0.800	0.640				
13	E.SPEC.		0.640	0.510				
14	A21489	0.740	0.520	0.420				
15	A2800/1	1.470	1.220	0.870				
16	A2800/2	1.700	1.340	0.980				
17	A2800/3	1.550	1.110	0.820				
18	A2800/4	1.200	0.800	0.520				
19	A2800/5	1.350	0.830	0.540				

f

Element % Tealliocaris

	Element	Pore canal	Epicuticle	Fibril	Exo. 5	Exo. 6	Exo. 7	Exo. 7'
1	Si	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1224
2	Ti	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1011
3	Fe	0.1536	0.0000	0.0000	0.1289	0.1852	0.1478	0.0000
4	Mg	0.6268	0.0000	0.0000	0.0000	0.1707	0.0000	0.0000
5	Ca	34.5209	31.8764	32.4712	32.5398	35.2357	33.8509	35.9366
6	Na	2.4827	0.4895	0.3070	0.4048	0.3408	0.0000	0.3150
7	K	0.0920	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
8	P	14.1634	13.6758	13.8962	13.8789	15.0053	13.8818	15.1210
9	S	0.2947	0.2119	0.1902	0.1453	0.1852	0.1422	0.1775

	Exo. 8	Exo. 9	Altered Cut.
1	0.0000	0.0000	0.0000
2	0.0000	0.0000	0.0000
3	0.0000	0.2270	0.1406
4	0.2098	0.2218	0.4965
5	36.6745	36.9353	38.0560
6	0.5347	0.6397	0.0000
7	0.0000	0.0000	0.0000
8	15.2035	15.1815	0.5399
9	0.1795	0.1924	0.2076

g

Fossil and Recent Crustacea

1. Tail fan: deltoid, rectangular or sub-rectangular;open (no uropodal membranes)
2. telson: triangular, subrectangular; complex (caudal furca,multiple caudal flaps);
3. 6th abdominal somite: longest; not longest;
4. 3rd abdominal somite: enlarged; undifferentiated from fourth;
5. 2nd abdominal pleura: enlarged to cover 1st and 2nd;undifferentiated;
6. 1st abdominal somite: shortest; undifferentiated;
7. pleopods: lamellate; flagellar;
8. carapace:yes; no;
9. cervical groove: T; U; 0;
10. rostrum: present; short or absent;
11. thoracopods undifferentiated: all; some;
12. thoracopods subchelate: none; some;
13. thoracopods: stenopods; flagellar;
14. epipods: large; absent or greatly reduced;
15. carapace: covers thorax; thoracic tergites visible;
16. antennules: 3 flagella; 2 flagella;
17. antennae: 2 flagella;single flagella;
18. thoracopods chelate: none; some;
19. seminal receptacle: present; absent;
20. number of "walking" thoracopods: <5; 5; 6; 7; 8;

```
"==Data===============123456789.....
"==========+==========1
Pygocephalus            01111170100001011002
Tealliocaris            00100000100000011011
Pseudogalathea          00111??01000?01101?
Crangopsis              00010100010001?11014
Kallidechthes           ???101?00100?1?1101?
Anthracophausia         000111?0?00001?1101?
Belotelson              000111?0?00001?11014
Anthracaris             01111107100001011002
Joanellia               00010100010001?1101?
Perimecturus            11111100101101101017
Bairdops                10111100101101101017
Pleurocaris             101111?121?000111014
Palaeocaris             101111?121?000111014
Praenaspides            101111?121?000111014
Minicaris               10111111217000111014
Anthracocaris           101111?011??1?1?0013
Palaemysis              00010100010011011013
Waterstonella           00010100010001111014
Decapod outgroup        00100000101000011011
&                          11   010  1   1
Mysid outgroup          00011100000000111002
&                         1      11?11    13
Syncarid outgroup       00111111210000111014
&                       1     0
Euphausiacean outgroup  00011100110001011014
&                         1      011    1
Stomatopod outgroup     11111100101101101010
&                        0       1
Tanaidacean outgroup    10111110111001110013
&                                1     1
Pygocephalomorph out    01111100100001011002
"10=========+===== ====================1
@
```

Cyclus and the Maxillipoda

1. Antenna: two flagella; one flagella;
2. Head shield with carapace: present; absent;
3. Subchelate limbs: 0; 1; 2;
4. 'walking' limbs: 4; 5; 0;
5. Abdominal somites: 5; >4;unsegmented;
6. Tail fan: caudal furca; cleft abdomen;
7. Antennules: short; long;
8. Antennules: 10 or less articles; greater than ten articles;
9. Sixth thoracopod in male: modified sex organ, not sex organ or short/absent;
10. Body form: elongate; ovate; highly modified;
11. Adaptation: mostly free living; modified parasitic;
12. Maxillules: developed as suckers; not suckers;
13. Body flexure between 6th thoracic somite and 1st abdominal somite: yes; no;

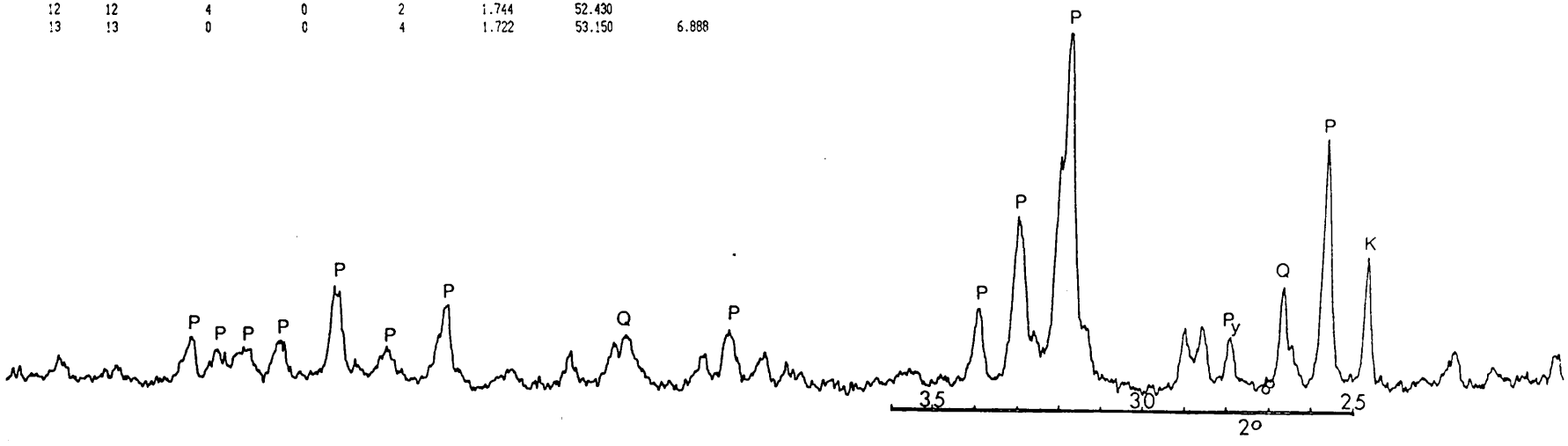
```
"==Data===============123456789.....
"==========+==========1

Cyclus                  10210011010107
Calanoida               11110011000117
&                             1
Misophrioida            10?1001111010
Harpacticoida           11?10000100107
Mormonilloida           11??701012110
Monstrilloida           11??701112110
Cyclopoida              11?1001111010
Poecilostomatoida       11??700012110
Siphonostomatoida       11??700012110
&                             11
Arguloida               10002100111007
"10=========+===== ====================1
@
```

h

XRD-cuticle phosphate

	peak no.	H	K	L	d	2theta	c	a
1	1	0	0	2	3.446	25.850	6.892	
2	2	1	0	2	3.170	28.150		
3	3	2	1	0	3.058	29.200		9.342
4	4	2	1	1	2.790	32.050		
5	5	3	0	0	2.696	33.200		9.339
6	6	2	0	2	2.620	34.200		
7	7	2	2	2	1.933	46.970		
8	8	3	1	2	1.878	48.430		
9	9	2	1	3	1.837	49.580		
10	10	3	2	1	1.791	50.950		
11	11	4	1	0	1.765	51.750		9.339
12	12	4	0	2	1.744	52.430		
13	13	0	0	4	1.722	53.150	6.888	



Crustacean Data

	Sample	Si	Al	Fe	Mg	Ca	Na	K	P	S	Cl	Ca/P
1	TPC	0.000	0.000	0.154	0.627	34.521	2.483	0.092	14.163	0.295	0.230	2.437
2	TP6	0.000	0.000	0.000	0.000	31.876	0.490	0.000	13.676	0.212	0.170	2.331
3	TP5	0.000	0.000	0.129	0.000	32.540	0.405	0.000	13.879	0.145	0.090	2.345
4	TP6	0.000	0.000	0.185	0.188	35.236	0.341	0.000	15.005	0.185	0.170	2.348
5	TP7	0.000	0.000	0.148	0.000	33.851	0.000	0.000	13.882	0.142	0.090	2.439
6	TP8	0.000	0.000	0.000	0.210	36.674	0.535	0.000	15.203	0.180	0.090	2.412
7	TP9	0.000	0.000	0.227	0.212	36.935	0.640	0.000	15.182	0.192	0.120	2.433
8	P1	0.000	0.000	0.199	0.000	30.496	0.286	0.000	13.140	0.249	0.000	2.321
9	P3	0.000	0.000	0.283	0.000	32.417	0.306	0.094	14.434	0.175	0.000	2.246
10	P5	0.000	0.000	0.135	0.000	30.477	0.000	0.000	13.471	0.283	0.000	2.262
11	P6	0.000	0.000	0.000	0.149	29.026	0.409	0.000	12.736	0.240	0.000	2.279
12	P7	0.138	0.000	0.228	0.133	31.638	0.427	0.082	13.547	0.200	0.000	2.335
13	P8	0.000	0.000	0.344	0.000	29.597	0.565	0.000	12.854	0.188	0.089	2.302
14	P9	0.000	0.000	0.144	0.215	34.199	0.638	0.000	14.965	0.210	0.075	2.285
15	P10	0.000	0.000	0.000	0.000	33.278	0.344	0.000	13.786	0.106	0.102	2.414
16	P11	0.000	0.000	0.157	0.196	31.383	0.571	0.000	13.265	0.091	0.097	2.366
17	P12	0.000	0.000	0.151	0.000	32.027	0.340	0.000	14.184	0.182	0.069	2.258
18	P13	0.000	0.000	0.296	0.144	31.350	0.429	0.000	13.665	0.186	0.092	2.294
19	P14	0.000	0.000	0.229	0.155	30.395	0.351	0.000	13.410	0.211	0.077	2.267
20	P15	0.120	0.000	0.271	0.000	31.773	0.000	0.000	13.710	0.264	0.076	2.318
21	B2	0.117	0.000	0.000	0.000	33.284	0.448	0.000	14.618	0.309	0.075	2.277
22	B3	0.099	0.000	0.135	0.000	32.176	0.638	0.000	14.009	0.219	0.000	2.297
23	B4	0.103	0.000	0.264	0.000	31.963	0.000	0.000	14.333	0.244	0.070	2.230
24	B5	0.210	0.000	0.198	0.000	31.003	0.000	0.000	13.474	0.342	0.000	2.301
25	B6	0.000	0.000	0.238	0.000	27.303	0.000	0.000	11.913	0.333	0.000	2.292
26	B7	0.104	0.000	0.206	0.167	31.007	0.000	0.000	13.904	0.319	0.000	2.230
27	B8	0.154	0.000	0.226	0.257	34.193	0.000	0.000	14.911	0.247	0.114	2.293
28	B9	0.000	0.000	0.000	0.000	16.971	0.318	0.000	7.470	0.331	0.000	2.272
29	B10	0.000	0.000	0.204	0.185	33.685	0.430	0.000	14.432	0.200	0.107	2.334
30	C1	0.000	0.000	0.000	0.000	32.179	0.000	0.000	14.266	0.000	0.129	2.256
31	C2	0.000	0.000	0.178	0.000	32.112	0.000	0.000	14.916	0.126	0.112	2.153
32	C3	0.000	0.000	0.148	0.000	33.198	0.000	0.000	14.805	0.000	0.117	2.242
33	C4	0.000	0.000	0.000	0.000	31.776	0.372	0.000	14.222	0.000	0.000	2.234
34	C5	0.000	0.000	0.000	0.000	32.514	0.000	0.000	14.577	0.000	0.123	2.231
35	C6	0.000	0.000	0.206	0.178	31.470	0.437	0.000	14.014	0.151	0.198	2.246
36	C7	0.000	0.000	0.148	0.000	31.211	0.000	0.000	14.395	0.000	0.143	2.168
37	C8	0.000	0.000	0.000	0.000	33.478	0.000	0.000	14.980	0.000	0.083	2.235
38	C9	0.116	0.000	0.230	0.000	32.024	0.000	0.000	14.273	0.149	0.249	2.244
39	C10	0.000	0.000	0.172	0.000	33.273	0.000	0.000	14.872	0.000	0.000	2.237
40	C11	0.000	0.000	0.161	0.137	31.966	0.000	0.000	14.427	0.092	0.176	2.216
41	C12	0.134	0.000	0.000	0.000	33.255	0.369	0.000	15.374	0.104	0.079	2.163
42	C13	0.000	0.143	0.231	0.132	31.760	0.000	0.000	13.995	0.134	0.158	2.269
43	C14	0.000	0.000	0.152	0.000	32.272	0.308	0.000	14.647	0.000	0.119	2.203
44	C15	0.100	0.000	0.148	0.135	32.064	0.000	0.000	14.385	0.000	0.129	2.229
45	C16	0.000	0.000	0.232	0.000	31.175	0.000	0.000	14.068	0.181	0.165	2.216
46	SED1	18.844	10.705	4.430	0.876	0.281	0.000	2.022	0.000	2.779	0.000	INF
47	SED 8C	22.352	5.208	1.077	0.354	0.080	0.000	1.037	0.000	0.148	0.093	INF
48	SED 99	25.347	7.961	1.954	0.682	0.098	0.000	1.612	0.000	0.575	0.000	INF
49	CX3	0.114	0.000	0.166	0.788	37.044	0.285	0.000	0.305	0.492	0.000	121.457
50	CX2	0.000	0.000	0.000	0.658	36.487	0.000	0.000	0.704	0.375	0.000	51.835
51	Tealliocaris(T) Mean	0.000	0.000	0.120	0.175	34.519	0.699	0.013	14.427	0.193	0.137	2.392
52	Palaemysis (P) Mean	0.020	0.000	0.187	0.076	31.389	0.357	0.014	13.628	0.199	0.052	2.304
53	Bairdops (B) Mean	0.087	0.000	0.163	0.068	30.176	0.204	0.000	13.229	0.283	0.041	2.281
54	Crangopsis (C) Mean	0.022	0.009	0.125	0.036	32.230	0.093	0.000	14.513	0.058	0.124	2.221
55	Sediment (SED) Mean	22.181	7.958	2.487	0.637	0.153	0.000	1.557	0.000	1.167	0.031	
56	Nodule (CX) mean	0.057	0.000	0.083	0.723	36.766	0.143	0.000	0.504	0.434	0.000	86.646

Salinity/Crustacean

	Na	Water	Na(1)	Inferred salinities(ppt)	Crustaceans
1	9.522	30.00	0.93	29.453	Crangopsis
2	11.100	34.80	1.43	30.932	Nodules
3	12.829	40.00	2.04	32.737	Bairdops
4		0.00	3.57	37.263	Palaemysis
5	10.760	35.00	6.99	47.381	Tealliocaris

Modern CRUST.

	Sample	Ca	P	S	Cl	Mg	Na
1	MC1	34.108	0.000	0.149	0.128	1.610	0.687
2	MC2	34.843	0.000	0.136	0.066	1.191	0.914
3	MC5	35.031	0.000	0.188	0.000	0.900	0.989
4	MC3	35.983	0.000	0.000	0.000	0.967	0.869
5	MC4	35.639	0.000	0.151	0.000	1.082	0.728
6	MC6	34.856	0.000	0.183	0.113	0.517	0.584
7	MC7	18.329	0.000	0.068	0.109	0.382	0.456
8	MC8	34.879	0.443	0.109	0.085	0.313	0.639
9	MC14	35.560	0.000	0.131	0.084	1.250	0.729
10	MC9	22.522	3.561	0.823	0.588	0.952	0.655
11	MC13	23.720	1.176	0.533	0.442	0.640	0.998
12	MC10	30.844	0.735	0.337	0.345	0.994	1.039
13	MC11	32.855	0.363	0.248	0.108	1.116	1.016
14	MC12	33.598	0.414	0.139	0.064	1.820	0.787

Other elements of the Manse Burn Formation fossil assemblages.

a) Bivalve spat dimensions. SM = Shrimp Member samples; PM = Posidonia Member samples (measurements in mm).

b) Orientation and position of *Palaemysis*. Based on data obtained during the major excavation (Shrimp Member). p = *Palaemysis*; (t) = tail fan; (a) = abdomen; (h) = anterior portion; c = *Cyclus*; F = fish.

c) Orientation and position of orthocones. Based on data obtained during the major excavation (Posidonia Member).

d) Orientation and position of sharks. Based on data obtained during the major excavation (Posidonia Member).

e) % composition of assemblage.

f) Graph showing the distribution of fossils collected during the major excavation.

g) Graphs of bivalve spat dimensions. SM = Shrimp Member; PM = Posidonia Member.

a

SM

	length of valve	width of valve	height		length of valve	width of valve	height
1	0.3139	0.3274		63	0.2915	0.3520	
2	0.2018	0.2466		64	0.2242	0.3229	
3	0.2197	0.2935		65	0.2332	0.3229	
4	0.2825	0.3475		66	0.2803	0.3812	
5	0.2668	0.3206		67	0.2825	0.3475	
6	0.2242	0.2668		68	0.2018	0.3139	
7	0.3296	0.3027		69	0.0830	0.1300	
8	0.2310	0.2866		70	0.2399	0.2960	
9	0.2130	0.2556		71	0.1054	0.1211	
10	0.2265	0.3055		72	0.2108	0.2780	
11	0.2691	0.2982		73	0.1906	0.2848	
12		0.3537	0.2242	74	0.2130	0.3004	
13	0.2534	0.2878		75	0.1794	0.2422	
14	0.2130	0.2623		76	0.2197	0.2915	
15	0.2242	0.3049		77	0.2758	0.2982	
16	0.2242	0.2242		78	0.2152	0.2735	
17	0.2578	0.3197		79	0.2399	0.2937	
18	0.2511	0.3184		80	0.2152	0.2960	
19	0.1345	0.1390		81	0.2354	0.2511	
20	0.1198	0.1507		82	0.2197	0.3341	
21	0.2242	0.3122		83	0.1457	0.2074	
22	0.2511	0.3274		84	0.1726	0.1794	
23	0.2354	0.3072		85	0.2130	0.2691	
24	0.0807	0.1031		86	0.2287	0.3139	
25	0.2354	0.3206		87	0.1099	0.1278	
26	0.1345	0.2026		88	0.0516	0.0650	
27	0.1839	0.2395		89	0.0942	0.1143	
28	0.2758	0.3694		90	0.1076	0.1256	
29	0.1787	0.2574		91	0.1278	0.1547	
30	0.0830	0.1117		92	0.2242	0.2691	
31	0.2242	0.3139		93	0.2422	0.3094	
32	0.2511	0.3049		94	0.2063	0.2780	
33	0.2444	0.2691		95	0.1177	0.1401	
34	0.2578	0.4058		96	0.1637	0.2287	
35	0.2915	0.3543		97	0.1457	0.2130	
36	0.1435	0.1637		98	0.1211	0.2018	
37	0.2623	0.3184		99	0.2332	0.3094	
38	0.2040	0.2657		100	0.0897	0.0942	
39	0.1188	0.1525		101	0.1771	0.2287	
40	0.0830	0.1121		102	0.1435	0.2018	
41	0.2803	0.3520		103	0.1009	0.1143	
42	0.2242	0.3211		104	0.2848	0.3520	
43	0.2220	0.3072		105	0.2803	0.3139	
44	0.1973	0.2691		106		0.3453	0.1704
45	0.2377	0.3161		107	0.2623	0.3924	
46	0.2466	0.2691		108	0.2175	0.3475	
47	0.0897	0.1233		109	0.2265	0.2691	
48	0.1973	0.2780		110		0.3206	0.1794
49	0.2915	0.3632		111	0.0717	0.1419	
50	0.2309	0.2825					
51	0.0650	0.0942					
52	0.0785	0.1009					
53	0.2466	0.3161					
54	0.0897	0.0942					
55	0.0874	0.1121					
56	0.1166	0.1345					
57	0.2108	0.2511					
58	0.2556	0.3184					
59	0.1861	0.2242					
60	0.1839	0.2489					
61	0.0807	0.0987					
62	0.0785	0.0897					

PM

PM spat data

	width	length	width	length
1	0.471	0.423	0.131	0.102
2	0.504	0.354	0.438	0.321
3	0.423	0.266	0.219	0.208
4	0.080	0.058	0.226	0.208
5	0.580	0.438	0.223	0.186
6	0.532	0.347	0.423	0.361
7	0.179	0.124	0.135	0.102
8	0.434	0.339	0.369	0.288
9	0.474	0.380	0.555	0.429
10	0.164	0.139	0.595	0.453
11	0.566	0.449	0.412	0.295
12	0.193	0.146	0.474	0.321
13	0.314	0.208	0.496	0.451
14	0.425	0.321	0.482	0.365
15	0.555	0.376	0.547	0.398
16	0.295	0.197	0.420	0.325
17	0.456	0.431	0.445	0.425
18	0.445	0.328	0.197	0.135
19	0.511	0.361	0.650	0.489
20	0.567	0.365	0.526	0.431
21	0.496	0.434	0.482	0.336
22	0.230	0.175	0.420	0.314
23	0.369	0.291	0.394	0.310
24	0.485	0.401	0.445	0.339
25	0.507	0.442	0.511	0.380
26	0.387	0.266	0.482	0.429
27	0.555	0.438	0.573	0.409
28	0.529	0.438	0.536	0.478
29	0.294	0.197	0.234	0.164
30	0.394	0.383	0.482	0.434
31	0.456	0.383	0.617	0.464
32	0.249	0.193	0.496	0.350
33	0.540	0.391	0.405	0.336
34	0.555	0.401	0.416	0.328
35	0.511	0.434	0.573	0.394
36	0.201	0.157	0.478	0.474
37	0.524	0.369	0.464	0.405
38	0.529	0.328	0.591	0.361
39	0.547	0.365	0.555	0.416
40	0.533	0.431	0.547	0.398
41	0.542	0.383	0.288	0.234
42	0.569	0.387	0.394	0.322
43	0.412	0.307	0.226	0.146
44	0.507	0.416	0.518	0.438
45	0.361	0.285	0.577	0.439
46	0.617	0.416	0.577	0.445
47	0.223	0.182	0.632	0.489
48	0.427	0.350	0.500	0.367
49	0.230	0.197	0.547	0.380
50	0.485	0.383	0.547	0.372
51	0.540	0.425	0.398	0.350
52	0.565	0.350	0.515	0.383
53	0.526	0.394	0.515	0.464
54	0.493	0.376	0.460	0.318
55	0.161	0.117	0.533	0.493
56			0.518	0.391

b

	object	angle	X	Y
1	p(t)	0.00	11.37	5.22
2	p(t)	0.00	13.40	3.80
3	p(t)	0.00	17.60	5.47
4	p(a)	0.00	16.20	2.90
5	c	0.00	19.31	3.98
6	p(t)	5.00	17.39	5.25
7	p(a)	8.00	17.64	5.65
8	p(t)	8.00	17.60	5.60
9	p(t)	20.00	9.65	4.77
10	p(t)	20.00	9.80	5.50
11	p(a)	20.00	10.38	5.35
12	p(a)	20.00	9.90	6.03
13	p(a)	20.00	11.16	5.24
14	p(a)	20.00	18.47	4.94
15	p(a)	30.00	10.44	4.30
16	p(t)	30.00	18.00	4.57
17	p(t)	30.00	18.04	4.63
18	p(a)	40.00	8.53	2.65
19	p(t)	40.00	19.45	3.50
20	p(a)	45.00	13.55	2.90
21	p(h)	45.00	17.50	5.40
22	p(a)	45.00	19.20	3.27
23	p(a)	50.00	8.50	2.62
24	p(t)	55.00	15.18	4.69
25	p(t)	65.00	9.45	2.44
26	p(t)	70.00	11.39	5.74
27	p(t)	85.00	11.10	6.48
28	p(t)	90.00	8.68	2.25
29	p(a)	90.00	13.40	3.80
30	p(a)	90.00	15.32	4.03
31	p(a)	90.00	16.05	2.92
32	p(t)	90.00	16.84	2.27
33	p(t)	90.00	18.25	4.48
34	p(t)	98.00	8.47	2.59
35	p(a)	100.00	10.22	3.82
36	p(t)	100.00	19.91	3.45
37	p(t)	110.00	11.39	5.60
38	p(a)	117.00	8.20	2.25
39	p(t)	120.00	8.60	3.23
40	p(t)	120.00	13.85	2.59
41	p(t)	120.00	15.50	4.10
42	p(t)	120.00	15.75	4.25
43	p(a)	120.00	17.62	5.40
44	p(t)	120.00	19.99	3.66
45	p(t)	125.00	9.15	2.30
46	c	130.00	11.01	5.25
47	p(t)	130.00	17.80	5.39
48	p(t)	140.00	11.88	5.02
49	p(a)	160.00	11.35	5.75
50	p(a)	160.00	19.95	3.47
51	c	180.00	13.28	2.84
52	p(h)	180.00	13.90	2.45
53	p(t)	180.00	15.80	4.10
54	p(t)	180.00	20.03	5.70
55	p(t)	182.00	13.70	3.70
56	p(t)	210.00	11.21	5.17
57	p(t)	210.00	18.39	4.65
58	p(t)	215.00	15.40	4.08
59	p(t)	240.00	13.70	2.30
60	p(t)	250.00	10.20	4.40
61	p(t)	260.00	8.15	2.60
62	p(t)	265.00	13.80	3.30
63	p(t)	270.00	13.50	2.90
64	F	270.00	15.20	4.90
65	p(t)	270.00	15.72	4.87
66	p(t)	290.00	20.55	5.10
67	p(h)	300.00	15.75	4.25
68	p(t)	300.00	19.16	3.24
69	p(h)	300.00	20.65	5.90
70	p(t)	315.00	11.48	5.57
71	p(t)	320.00	17.30	5.30
72	p(t)	330.00	11.81	5.13
73	p(t)	340.00	10.40	6.10
74	p(t)	340.00	10.53	6.18
75	p(h)	340.00	10.52	6.15
76	p(a)		9.30	6.00
77	p(t)		9.70	5.60
78	p(t)		9.70	5.40
79	p(a)		11.40	5.70
80	p(a)		11.55	5.54
81	p		11.52	5.12
82	p		11.92	5.57
83	p		13.50	3.50
84	p		13.15	2.75
85	p		18.25	4.00
86	p		19.60	3.53
87	p		19.45	3.60
88	p		19.35	3.35
89	p		20.80	5.64
90	p		20.20	5.90

C

	X	Y	angle	length
1	10.10	2.47	0	5.0
2	15.57	4.48	0	2.5
3	17.38	4.57	0	4.0
4	18.12	2.11	0	3.5
5	15.86	4.25	5	11.0
6	15.68	2.64	10	5.5
7	13.45	4.41	30	2.5
8	15.26	4.85	30	11.0
9	21.18	5.50	45	2.0
10	21.73	4.61	60	2.5
11	16.65	3.31	70	3.0
12	19.63	5.16	70	2.0
13	11.84	2.97	75	7.0
14	18.92	5.03	75	3.5
15	21.26	4.82	75	11.0
16	13.60	6.31	80	12.0
17	15.28	3.74	80	2.5
18	21.20	5.58	80	5.0
19	19.88	6.66	85	2.5
20	17.78	6.05	90	5.0
21	17.11	5.38	95	2.5
22	21.56	5.30	100	7.5
23	21.87	5.28	105	5.0
24	12.49	4.60	120	5.0
25	21.16	4.19	125	3.0
26	14.39	6.42	130	1.5
27	12.41	6.46	140	2.5
28	20.14	6.63	140	4.0
29	19.82	2.74	140	2.5
30	19.95	2.39	140	6.0
31	12.69	5.96	150	3.0
32	12.66	3.46	150	3.0
33	11.90	5.69	160	14.0
34	16.33	4.62	175	10.5
35	21.39	5.37	175	4.0
36	11.14	6.38	180	2.0
37	19.06	4.78	190	8.0
38	21.78	5.63	195	11.0
39	12.07	2.41	200	3.0
40	18.32	4.68	205	5.0
41	14.87	4.37	210	4.0
42	15.92	2.68	210	0.5
43	14.15	5.36	220	2.0
44	14.33	2.86	220	5.0
45	19.82	3.36	220	5.0
46	21.83	4.83	225	5.0
47	12.65	5.05	230	2.0
48	16.16	3.85	235	6.0
49	19.04	6.33	240	2.0
50	14.60	3.30	240	6.5
51	20.53	2.17	240	6.5
52	21.16	5.35	240	7.5
53	16.20	6.76	250	6.0
54	16.28	6.63	250	3.0
55	15.82	2.56	250	5.5
56	21.10	5.44	250	4.5
57	19.02	2.12	260	6.0
58	11.81	3.94	265	10.0

X	Y	angle	length	nature
16.890	6.200	270.000	13.000	
21.890	6.310	275.000	2.000	
18.580	3.420	275.000	7.000	
12.620	3.520	280.000	2.000	
13.410	5.270	280.000	5.000	
16.350	2.070	290.000	5.000	
12.300	4.550	300.000	3.000	
14.700	4.510	300.000	18.000	
18.050	2.220	300.000	17.000	
21.650	3.360	300.000	1.000	
19.970	3.405	310.000	5.000	ribbed
13.410	2.200	315.000	3.000	
14.510	3.550	320.000	4.500	
16.750	3.820	320.000	13.000	
18.400	5.572	320.000	4.000	
21.760	3.890	320.000	1.500	
21.380	5.410	325.000	3.500	
12.210	6.360	330.000	3.000	
17.050	5.150	330.000	12.000	
20.500	2.460	335.000	9.000	
10.500	3.520	340.000	5.000	
20.640	6.370	340.000	2.000	
13.110	3.920	340.000	3.500	
14.160	4.950	340.000	9.000	
13.580	5.850	350.000	1.500	
15.890	5.920	355.000	2.000	
19.630	2.500	355.000	10.000	ribbed
20.350	5.600		5.000	coiled
10.350	5.820		4.000	coiled

d

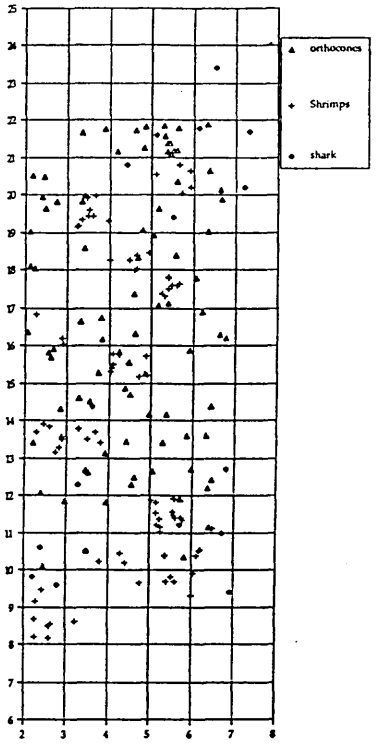
	Sharks	X	Y	angle
1	cl	9.400	6.900	315.000
2	cl	9.600	2.800	45.000
3	de	9.800	2.200	315.000
4	cl	10.500	3.500	
5	cl	10.600	2.400	45.000
6	cl	11.000	6.700	225.000
7	cl	11.200	5.700	315.000
8	cl	12.300	3.300	
9	cl	12.700	6.800	270.000
10	cl	14.400	3.600	265.000
11	cl	19.400	5.500	190.000
12	cl	20.800	4.400	40.000
13	cl	21.600	5.100	
14	cl	23.400	6.500	165.000
15	cl	21.800	6.100	140.000
16	cl	21.700	7.300	200.000
17	de	20.200	7.200	140.000

e

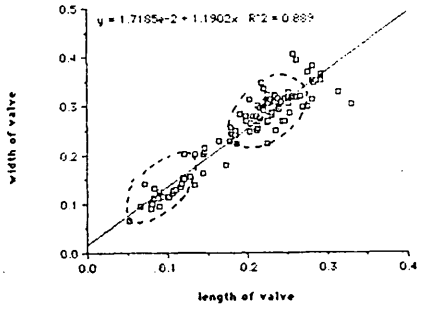
Bearsden Fauna%

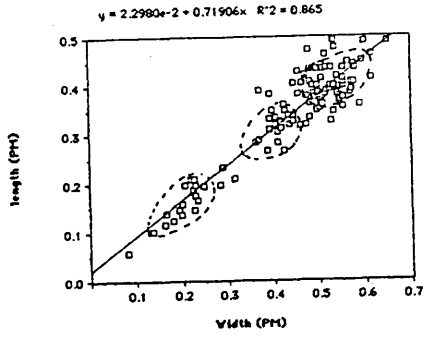
	Sample	Posidonia	Modiolus	Nucula	Pecten	Gastrop.(flat)	Gastrop(high)	Plant debris
1	134	0.000	0.000	36.232	3.623	28.986	7.246	5.797
2	75	0.450	0.000	90.290	0.000	2.260	0.000	2.260
3	65	3.500	0.200	1.060	0.000	95.200	0.000	0.000
4	85	0.000	0.000	44.640	1.786	44.640	0.000	8.930
5	45	23.810	1.587	3.175	15.873	55.556	0.000	0.000
6	35	0.000	0.000	44.248	2.655	44.248	0.000	8.850
7	55	4.167	1.042	1.042	0.000	93.750	0.000	0.000
8	95	0.000	0.000	0.000	8.333	0.000	0.000	41.667
9	105	0.000	0.000	51.546	0.000	41.237	0.000	5.155
10	25	0.000	6.818	0.000	0.000	0.000	0.000	11.364
11	115	0.000	0.000	0.000	0.000	0.000	0.000	16.327

	Lingula	Fish Debris	Naladites	Conodonts	Crangopsis	Ostracods
1	4.348	2.174	7.246	0.725	0.000	3.623
2	4.510	0.226	0.000	0.000	0.000	0.000
3	0.000	0.000	0.000	0.000	0.000	0.000
4	0.000	0.000	0.000	0.000	0.000	0.000
5	0.000	0.000	0.000	0.000	0.000	0.000
6	0.000	0.000	0.000	0.000	0.000	0.000
7	0.000	0.000	0.000	0.000	0.000	0.000
8	20.833	4.167	25.000	0.000	0.000	0.000
9	0.000	2.062	0.000	0.000	0.000	0.000
10	0.000	11.364	22.727	2.273	45.455	0.000
11	20.408	2.041	61.224	0.000	0.000	0.000


orthocones
Shrimps
shark

f


y = 1.7185e-2 + 1.1902x R^2 = 0.889
width of valve
length of valve


y = 2.2980e-2 + 0.71906x R^2 = 0.865
length (PH)
Width (PH)

g

Chemistry of the Sediments.

a) Trace element chemistry of the Manse Burn Formation. SM = Shrimp Member; THL = Top Hosie Limestone; PM = Posidonia Member; NSM = Nodular Shale Member; NASC = North American Shale Composite; A/N = phosphatic nodule; A/N2 = phosphatic nodule after dialysis; NaCl = salt used in dialysis experiment.

b) Comparison of rare earth elements.

c) XRD-traces of Manse Burn Formation shales. From the Shrimp Member: PG = Powgree Burn; CB = Corrie Burn; MB = Manse Burn; HG = Hindog Glen; BW = Bridge of Weir; RCB = Red Cleugh Burn; SG = Swinlees Glen; BB = Burniebrae Burn;

Other Members: E = Lingula Member; D = Platey Shale Member; C = Nodular Shale Member; B = Posidonia Member; H = Top Hosie Limestone and marine shale.

d) % area of XRD-trace peaks for different minerals.

a

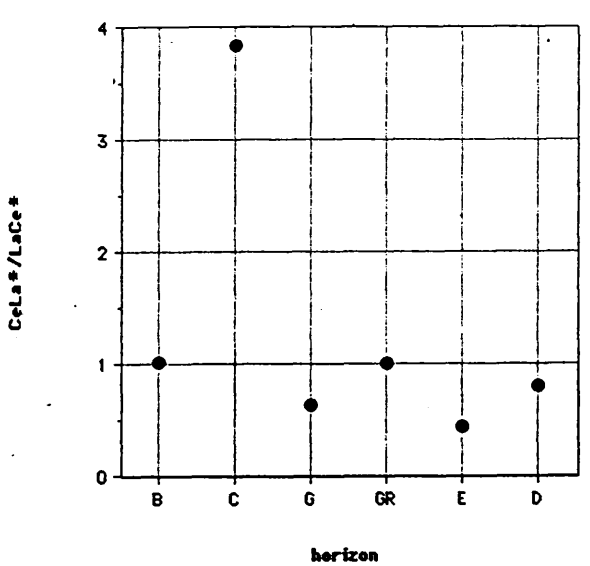
	Elements (ppm)	SH	THL	PH	black mud (KSE)	coprolite1	coprolite2	"NASC"	A/H	A/K2	AN/AK2
1	Zr	94	83	109	95	89	37	200	115	113	1.018
2	Y	31	44	47	15	2726	790		777	870	0.893
3	Sr	132	712	158	99	1161	416	142	688	724	0.950
4	U	11	3	18	11	10	9	3	27	28	0.964
5	Rb	131	21	58	117	1	1	125	38	41	0.927
6	Th	13	8	8	4	0	2	12	2	1	2.000
7	Pb	39	33	39	60	28	12		16	25	0.640
8	Ga	21	5	22	25	0	2		8	10	0.800
9	Zn	93	53	416	20	73	960		184	239	0.770
10	Cu	53	23	90	0	64	36		18	78	0.231
11	Ni	65	49	107	14	53	23	58	27	33	0.818
12	Co	26	31	44	3	44	7	26	19	21	0.905
13	Cr	104	38	137	101	0	0	124	16	15	1.067
14	Ce	93	93	85	64	2356	275	67	1090	1208	0.902
15	Ba	257	156	216	215	7609	286	636	0	0	1.000
16	La	46	33	39	39	523	23	31	504	552	0.913

	Element	L. Lavas	U. Lavas	Vents	Bearsden Shales (Av.)	phos. nod. SH	C 1	C2	NASC	A/K2 (SH)	NaCl
1	Ba	552.0	677.9	442.7	236.5	0.0	7609.0	286.0	636.0	0.0	26.0
2	Ce	98.1	107.4	76.7	89.0	1090.0	2356.0	275.0	66.7	1208.0	0.0
3	Co	35.0	22.0	53.5	35.0	19.0	44.0	7.0	25.7	21.0	0.0
4	Cr	16.1	27.3	27.5	120.5	16.0	0.0	0.0	124.5	15.0	5.0
5	Cu	16.5	29.9	18.5	71.5	18.0	64.0	36.0		78.0	19.0
6	Ga	24.1	28.0	27.6	21.5	8.0	0.0	2.0		10.0	1.0
7	La	40.5	49.3	29.6	42.5	504.0	523.0	23.0	31.1	552.0	0.0
8	Ni	19.7	20.9	32.0	86.0	27.0	53.0	23.0	58.0	33.0	16.0
9	Pb	7.1	11.1	4.5	39.0	16.0	28.0	12.0		25.0	1.0
10	Rb	32.1	57.0	30.4	94.5	38.0	1.0	1.0	125.0	41.0	1.0
11	Sr	804.1	418.3	784.4	145.0	688.0	1161.0	416.0	142.0	724.0	5.0
12	Th	5.8	8.7	5.1	10.5	2.0	8.0	2.0	12.3	1.0	2.0
13	Y	33.6	43.0	30.3	39.0	777.0	2726.0	790.0		870.0	8.0
14	Zn	107.9	127.8	92.2	254.5	184.0	73.0	960.0		239.0	6.0
15	Zr	310.0	428.8	256.2	101.5	115.0	89.0	37.0	200.0	113.0	6.0

b

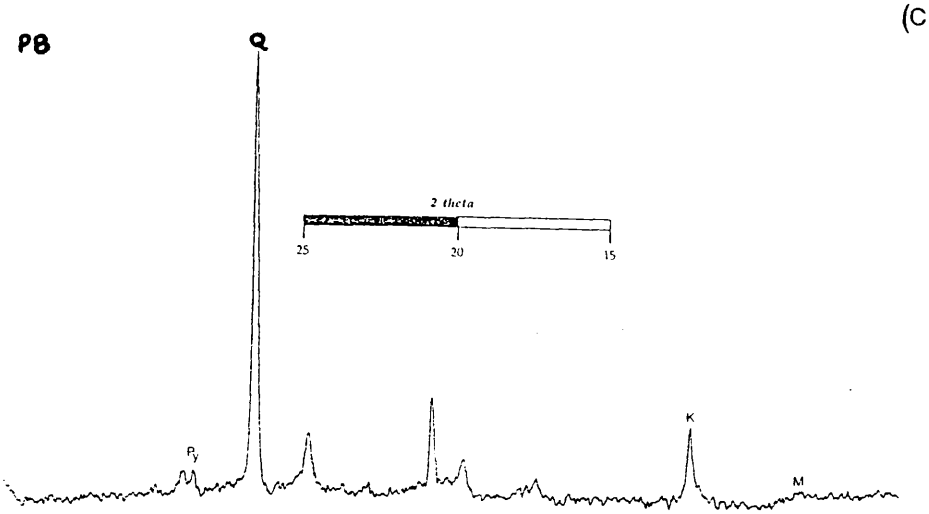
Comparative Trace Elem.

	Horizon	horizon	Ce (ppm)	La (ppm)	Locality	Ce/La	CeLa*/LaCe*
1	SM	A	93	46	B	2.022	0.942
2	THL	Lst	93	33	B	2.818	1.313
3	PM	D	85	39	B	2.179	1.015
4	black mud (NSM)	BM	64	39	B	1.641	0.765
5	coprolite1	C1	2356	523	C	4.505	2.099
6	coprolite2	C2	275	23	C	11.957	5.572
7	Grandjean '87	P1	176	65	G	2.708	1.262
8		P3	165	259	G	0.638	0.297
9		P4	672	544	G	1.235	0.576
10		P5	1135	471	G	2.410	1.123
11		P7	600	243	G	2.469	1.151
12		P8	1007	719	G	1.401	0.653
13		P9	151	148	G	1.020	0.475
14		P10	242	99	G	2.435	1.135
15		P11	14	20	G	0.707	0.329
16		P12	503	282	G	1.784	0.831
17		P13A	30	51	G	0.601	0.280
18		P13B	21	45	G	0.473	0.220
19		P14	13	43	G	0.302	0.141
20		P15	10	7	G	1.398	0.651
21		P16	9	8	G	1.086	0.506
22		P16a	108	82	G	1.318	0.614
23		P16b	131	96	G	1.368	0.637
24		P16c	134	110	G	1.218	0.568
25		P16d	53	37	G	1.429	0.666
26		P16e	46	34	G	1.353	0.630
27		A16	175	75	G	2.333	1.087
28		P16f	61	73	G	0.836	0.390
29		P21	1390	1052	G	1.321	0.616
30		P18b	30	28	G	1.060	0.494
31		P19	549	468	G	1.173	0.547
32		P20	1	1	G	1.994	0.929
33		P22	30	16	G	1.955	0.911
34	Gromet '84	"NASC"	67	31	GR	2.145	1.000
35	Elderfield	Sea Water	66	37	E	1.807	0.842
36			17	13	E	1.292	0.602
37			22	17	E	1.312	0.611
38			18	22	E	0.818	0.381
39			25	25	E	0.980	0.457
40			10	21	E	0.463	0.216
41			21		E		
42			10	23	E	0.426	0.199
43			26	29	E	0.888	0.414
44			19	33	E	0.592	0.276
45			55	54	E	1.013	0.472
46	De Baar	Seawater 2	86	15	D	5.733	2.672
47			80	12	D	6.667	3.107
48			42	12	D	3.415	1.591
49			30	13	D	2.326	1.084
50			23	17	D	1.377	0.642
51			18	18	D	1.011	0.471
52			16	21	D	0.751	0.350
53			15	22	D	0.676	0.315
54			23	27	D	0.846	0.394
55			15	26	D	0.573	0.267
56			14	26	D	0.534	0.249
57					D		
58			20		D		
59			16	47	D	0.343	0.160
60			44	84	D	0.525	0.245
61			44	81	D	0.545	0.254



(C)

PB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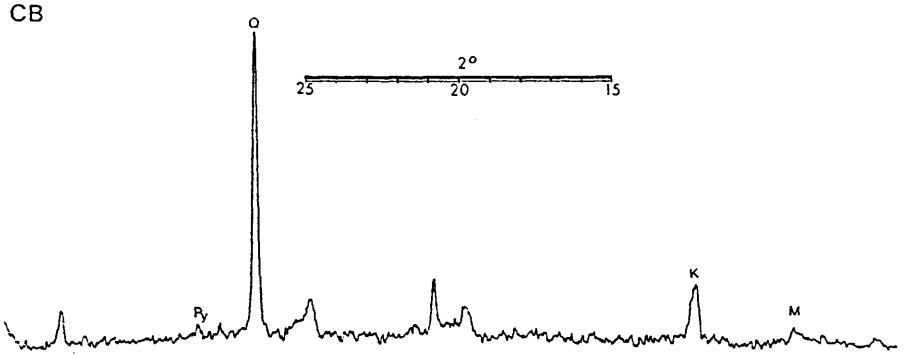
2 theta
25
20
15
Py
K
M

CB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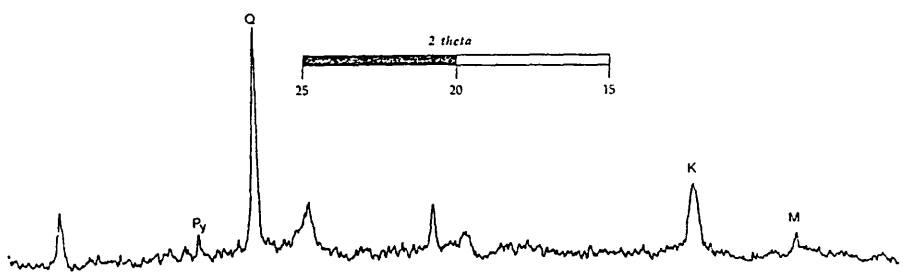
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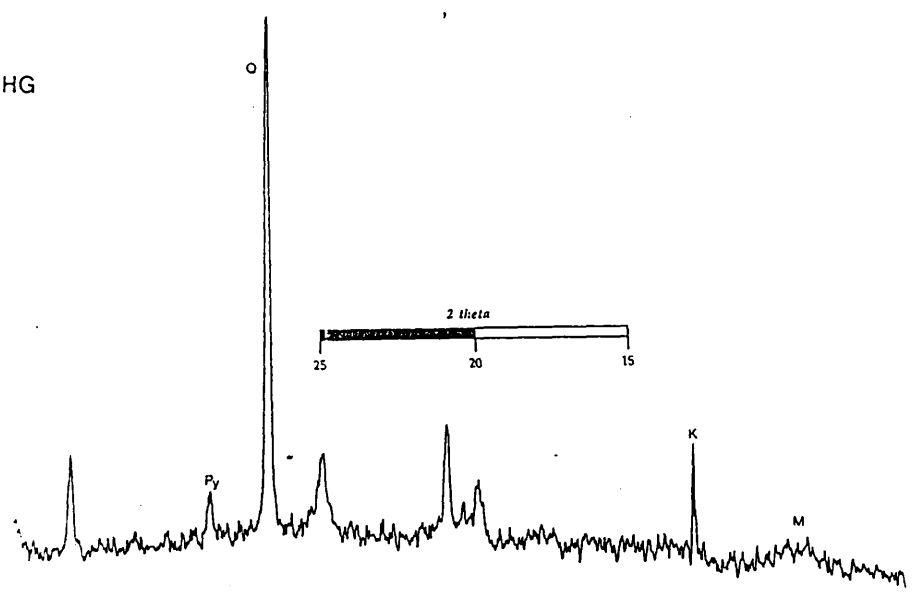
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Py
K
M

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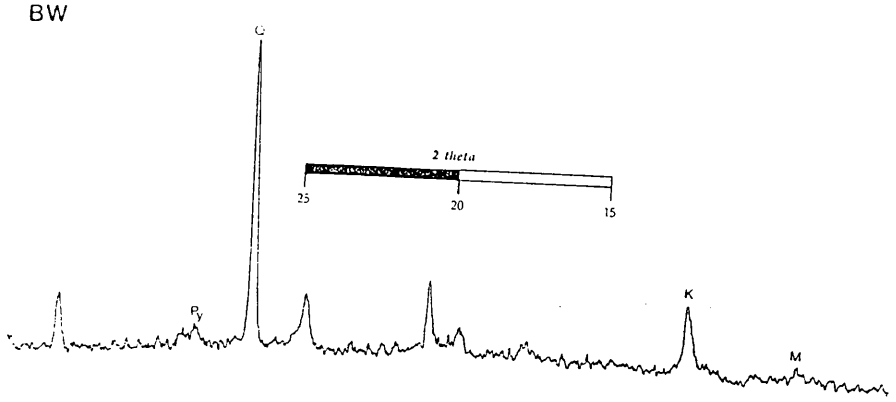
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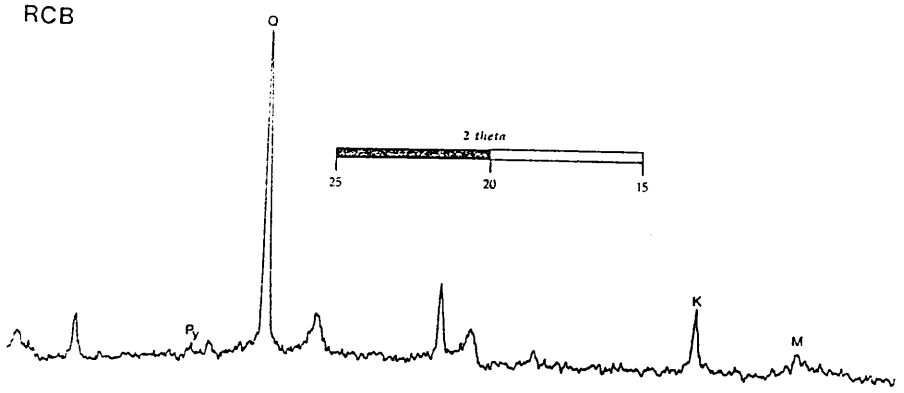
K
M

RCB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2 theta
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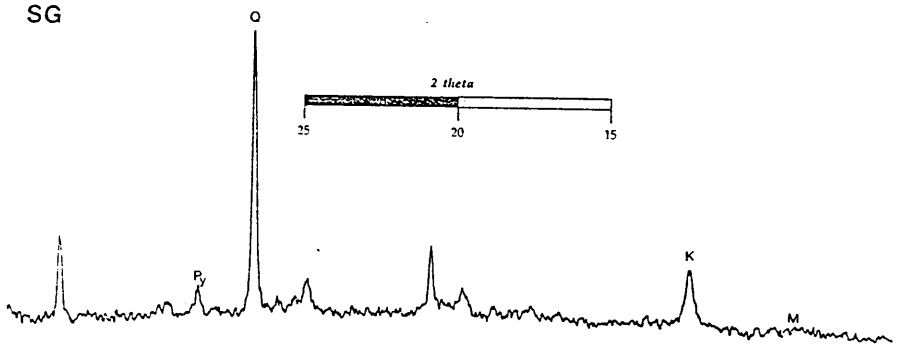
20
15
Py
K
M

SG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2 theta
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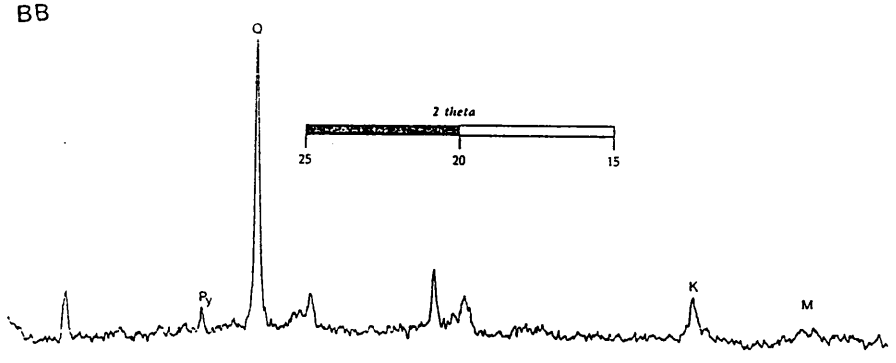
20
15
Py
K
M

BB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Py
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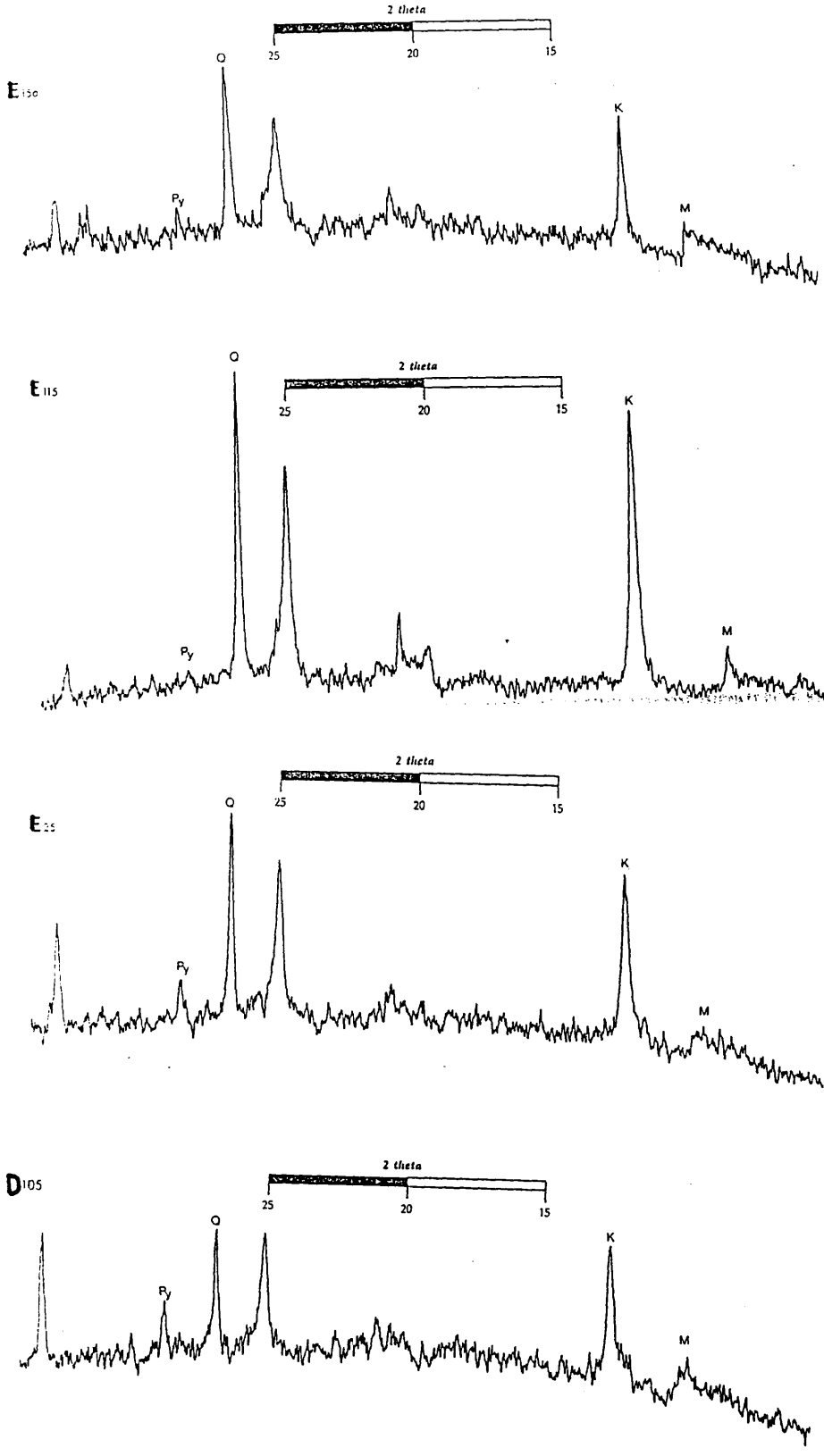
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20
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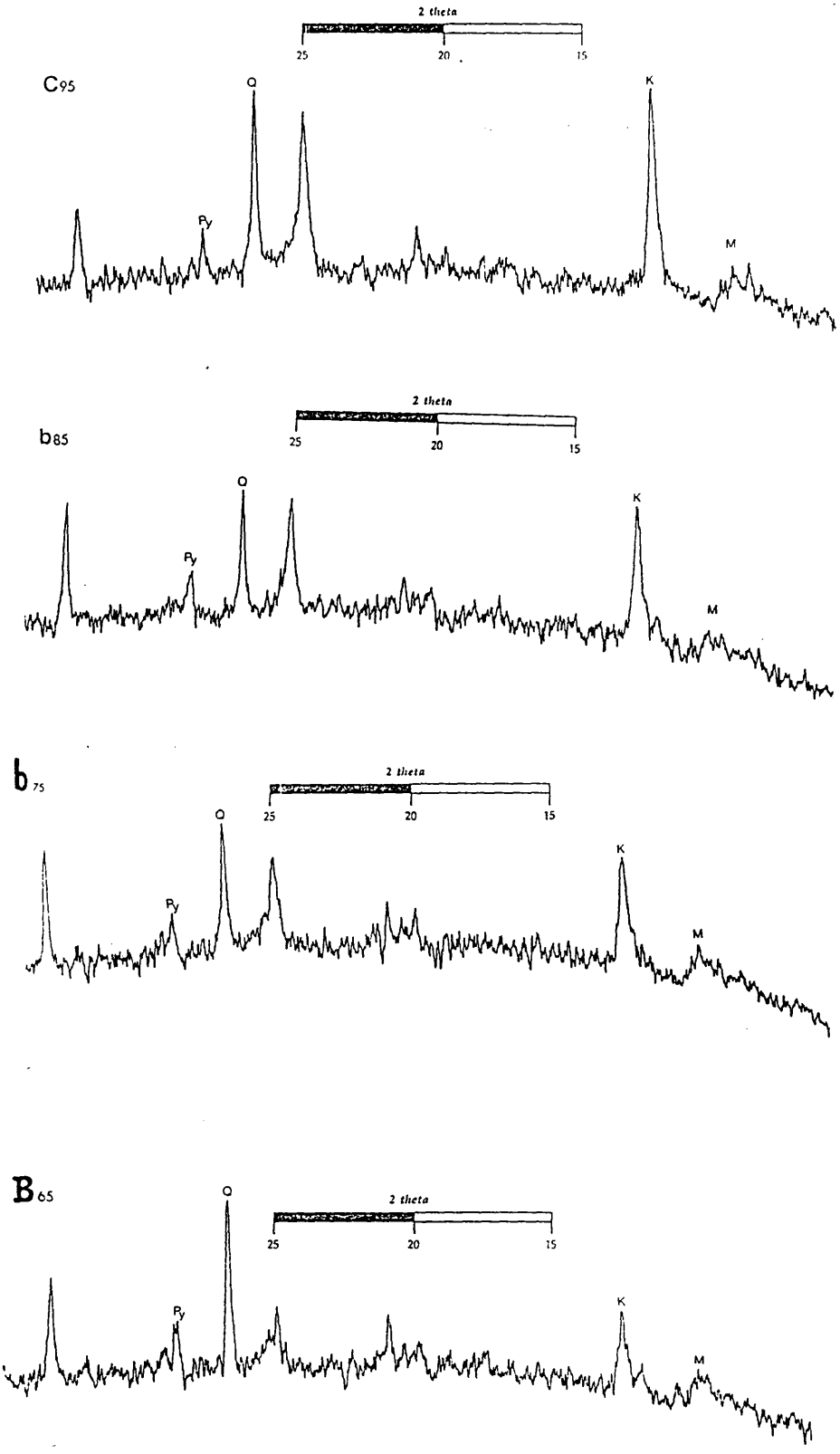
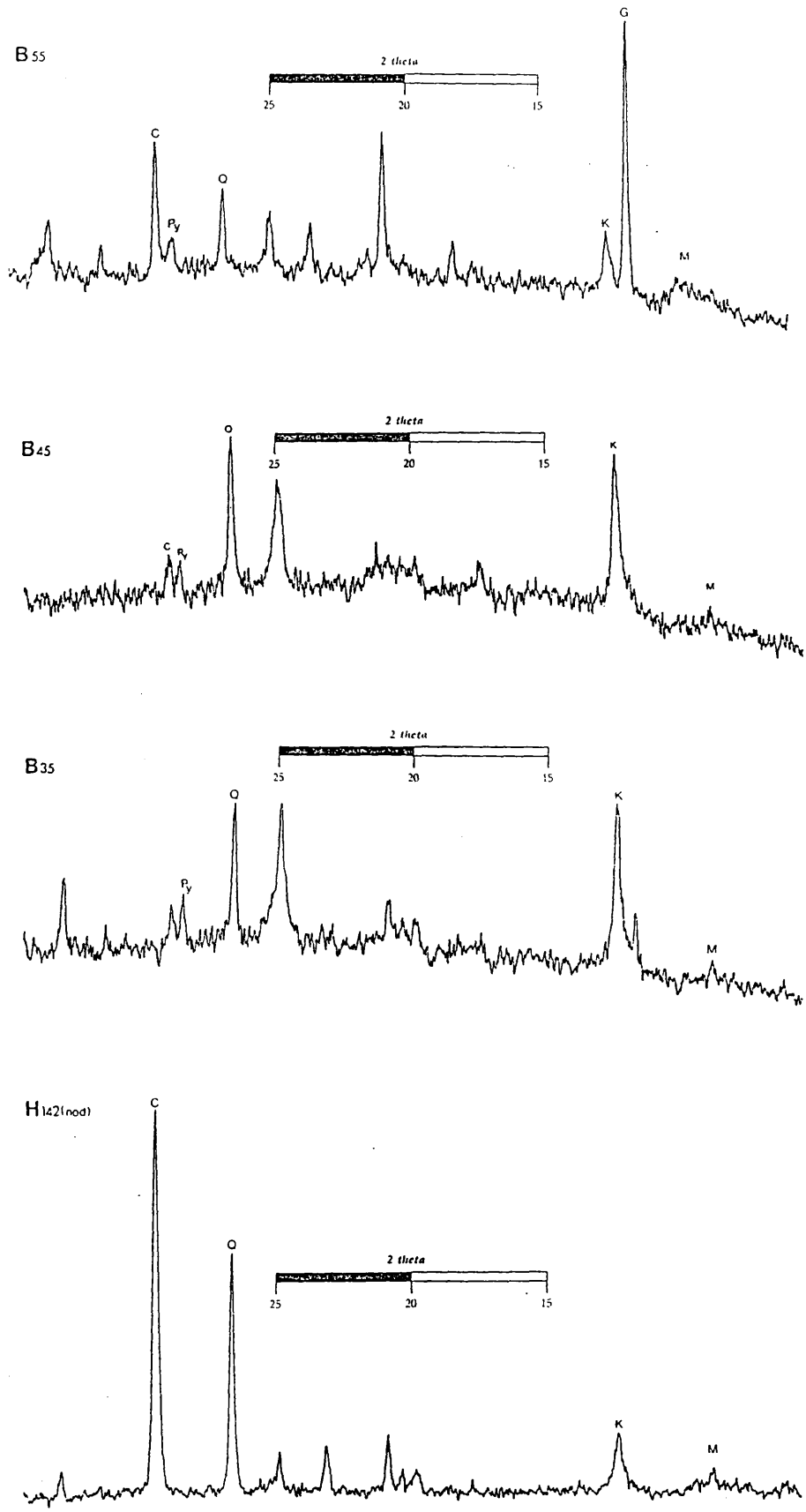
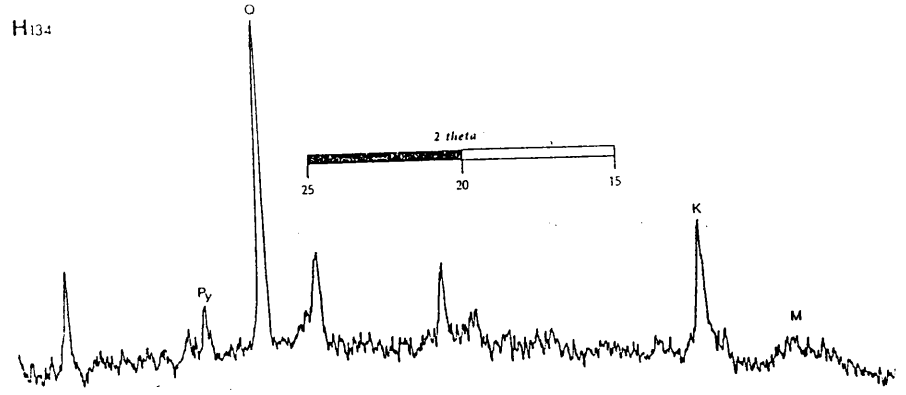
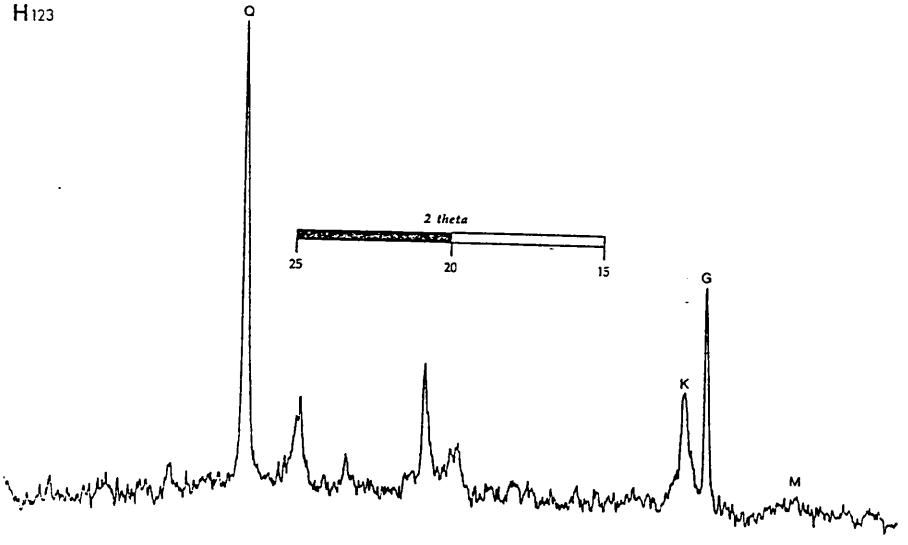
M
Py
E150
E115
E25
D105


2 theta
25
20
15
C95
Q
K
Py
M
2 theta
25
20
15
b85
Q
K
Py
M
b75
2 theta
25
20
15
Q
K
Py
M
B65
Q
2 theta
25
20
15
K
Py
M


B 55
2 theta
25
20
15
C
Py
O
K
G
M
B45
2 theta
25
20
15
O
C
Py
K
M
B35
2 theta
25
20
15
O
Py
K
M
H142(nod)
C
O
2 theta
25
20
15
K
M


H134
Q
2 theta
25
20
15
K
Py
M


H123
Q
2 theta
25
20
15
G
K
M

d

Area % B'den seds

	Muscovite	Kaolinite	Quartz	Pyrite	Calcite	Phosphate	Sample
1	8.245	28.381	60.335	3.039	0.000	0.000	BH123%
2	6.262	31.697	52.532	9.509	0.000	0.000	BH134%
3	7.740	20.768	58.900	2.856	9.736	0.000	BH142s%
4	5.270	11.236	32.853	4.494	46.146	0.000	BH142n%
5	7.429	20.471	66.271	5.829	0.000	0.000	Mean SM
6	10.280	24.663	54.984	10.073	0.000	0.000	BA1%
7	4.783	24.335	61.595	9.287	0.000	0.000	BA165%
8	10.130	49.959	27.175	12.736	0.000	0.000	BB35%
9	7.214	42.224	33.673	16.890	0.000	0.000	BB45%
10	8.701	51.058	40.241	0.000	0.000	0.000	BB55%
11	8.985	28.986	42.319	19.710	0.000	0.000	BB65%
12	7.956	38.892	33.589	19.563	0.000	0.000	BB75%
13	9.203	45.282	26.468	19.047	0.000	0.000	B385%
14	10.937	47.785	29.908	11.370	0.000	0.000	BC95%
15	9.002	45.910	27.853	17.235	0.000	0.000	BD105%
16	7.818	46.910	31.869	13.403	0.000	0.000	BE25%
17	8.374	49.626	38.205	3.795	0.000	0.000	BE115%
18	10.101	44.613	36.532	8.754	0.000	0.000	BE156%

Enterospire data

a) Probe analyses of enterospiral contents. F = fish fragments; SED = sediment surrounding enterospire; B = bivalves; PF = pore filling cement; P = pyrite, sphalerite, bayrite; C = enterospire groundmass; NOD = crustacean bacterial nodule; GUT = inter-whorl cement; CRUST = crustacean calcite nodules and associated cuticle.

Section

NCA1: C1, PF1, B1, SED1, B2, B2R, B3, F1, F2, F3, BB1, CA.

NCB1: FT1, PF2, F4, FT2, F6, F7, F8, F9, F10, F11, BB2, F12, F13, P1, P2, CB1, CB2, NOD1, NOD2, NOD3.

NCC1: D1, BB3, F14, B4, F15, F16, F17, CC1, PF3.

NCC2: NCC2, GUT1, P1, NCC3, FN1, FN2, PF1, PF2, F18, F19, F20, F21, F22.

NCA2: PF4, PF5, PF6, F23, F24, F25, P3, P4, C2, C3, P5, P6.

NCB2: P7, PF6, PF7, C4, PF8.

NCC3: CRUST1, PF9, F26, PF10, SED2, SED3, C1, PF11.

NCB4: C1, C2P, C2, C3, C4, C5, C6, C6P (amphipolar crustacean coprolites).

NCA3: P12, F27, SED4, SED5.

NCA4: C2, PF13, F28, F29, C3, SED6.

NCB3: PF14, PF15, F30E, F31E, F32E, F33E, PF16, F34E, F35E, F36E, F37E, F38E, F39E, C4, SED7.

NC-1-ABC: SED8C, SED9D, CRUST2, CRUST3, CRUST4, CRUST5, CRUST6, CRUST 7, AV SED10.

b) Enterospire dimensions. Tl = total length; mt = maximum width; lmt = maximum length to maximum width; nt = nodule thickness. (measurements in mm).

a

probe coprol. %elemt.

	Element	C1	PF1	B1	SED1	B2	B2R
1	Si	1.830	18.859	19.458	5.327	5.364	2.842
2	Al	0.825	13.344	13.962	2.618	2.537	0.330
3	Ba	0.523	0.000	0.135	0.000	0.219	0.000
4	Fe	0.641	0.699	0.545	1.314	0.348	0.128
5	Ca	15.123	3.331	1.054	16.022	4.469	11.995
6	Mg	1.038	0.163	0.280	0.495	0.476	0.279
7	Mn	0.000	0.000	0.000	0.000	0.000	0.000
8	Na	0.473	1.931	1.724	0.354	1.815	0.416
9	K	0.197	0.285	1.323	0.552	0.330	0.000
10	P	5.137	0.000	0.000	7.760	0.000	6.396
11	S	0.254	0.088	0.142	0.000	0.399	0.067
12	Cl	1.551	0.000	0.389	0.000	0.686	0.000
13	Ni	0.000	0.000	0.000	0.000	0.000	0.000

	B3	F1	F2	F3	BB1	CA	FT1
1	0.160	3.879	0.000	0.000	19.682	0.613	4.280
2	0.000	1.056	0.000	0.000	0.000	0.299	1.438
3	0.000	0.000	0.000	0.000	0.000	0.149	0.000
4	0.167	0.412	0.000	0.131	0.000	0.000	0.406
5	7.822	21.844	6.216	15.825	0.169	10.947	12.442
6	0.167	0.249	0.000	0.217	0.000	0.344	0.723
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.458	0.393	0.796	0.695	0.000	0.548	0.591
9	0.092	0.112	0.000	0.000	0.000	0.122	0.779
10	0.193	2.530	9.116	9.149	0.000	5.836	4.719
11	0.269	0.374	0.161	0.141	0.263	0.072	0.220
12	0.318	0.316	0.000	0.000	0.000	0.256	0.071
13	0.000	0.000	0.000	0.000	0.000	0.000	0.000

probe coprol. %elemt.

	PF2	F4	F5	FT2	F6	F7	F8
1	6.537	5.551	0.095	0.148	18.949	17.041	0.000
2	5.908	0.901	0.000	0.116	0.438	5.929	0.000
3	0.126	1.002	0.000	0.000	0.108	0.000	0.000
4	0.201	0.371	0.000	0.224	0.213	1.172	0.000
5	1.823	17.435	15.830	22.106	14.533	7.945	14.971
6	0.779	2.455	0.161	0.191	0.286	0.772	0.000
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.360	0.413	0.392	0.720	0.000	0.944	0.527
9	0.398	0.654	0.000	0.000	0.093	5.553	0.000
10	0.000	8.139	9.171	10.254	5.289	3.397	8.773
11	0.230	0.121	0.000	0.760	0.156	0.000	0.086
12	0.370	0.170	0.087	0.268	0.356	0.000	0.000
13	0.000	0.000	0.000	0.144	0.000	0.000	0.000

	F9	F10	F11	BB2	F12	F13	P1
1	0.000	25.720	0.000	8.694	0.260	0.000	3.845
2	0.000	0.491	0.000	3.055	0.000	0.000	1.263
3	0.000	0.000	0.000	0.269	0.000	0.078	0.823
4	0.000	0.218	0.000	1.769	0.000	0.000	2.649
5	22.833	9.797	16.180	14.418	9.695	8.286	12.434
6	0.000	0.000	0.000	1.061	0.000	0.114	2.514
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.402	0.420	0.000	2.328	0.577	0.342	0.495
9	0.000	0.000	0.000	0.220	0.000	0.000	0.217
10	11.683	4.502	9.287	3.917	6.291	5.980	1.507
11	0.141	0.247	0.166	0.391	0.000	0.065	2.351
12	0.000	0.068	0.000	1.549	0.000	0.000	3.873
13	0.000	0.000	0.000	0.000	0.000	0.000	0.000

	P2	CB1	CB2
1	0.961	3.320	7.714
2	0.441	1.194	1.133
3	0.000	0.218	0.232
4	4.679	0.512	1.102
5	2.632	16.648	10.679
6	0.000	0.839	1.572
7	0.000	0.000	0.000
8	0.000	0.538	0.413
9	0.069	0.170	0.326
10	0.284	6.732	3.424
11	14.201	0.253	0.223
12	0.000	0.704	0.619
13	0.000	0.000	0.000

	Element	D1	BB3	F14	D4	F15	F16	F17	PF1	PF3
1	Si	0.857	3.336	0.089	16.309	19.070	0.000	0.000	2.289	7.345
2	Al	0.313	1.461	0.000	12.839	10.702	0.000	0.000	0.294	5.516
3	Ba	0.000	0.000	0.000	0.070	0.092	0.000	0.000	0.000	0.897
4	Fe	1.577	1.500	0.110	0.596	0.512	0.000	0.000	0.431	4.531
5	Ca	25.272	22.295	22.104	1.335	9.673	14.555	15.787	17.416	1.868
6	Mg	0.953	0.650	0.127	0.553	0.256	0.000	0.000	0.404	1.208
7	Mn	0.000	0.180	0.000	0.000	0.000	0.000	0.000	0.000	0.102
8	Na	0.000	0.302	0.433	1.207	3.829	0.805	0.578	0.000	1.896
9	K	0.000	0.144	0.242	0.603	0.306	0.079	0.078	0.000	0.518
10	P	0.000	0.000	11.046	0.000	2.230	8.647	9.426	5.548	0.392
11	S	0.000	0.297	0.176	0.000	0.087	0.080	0.113	0.000	1.043
12	Cl	0.000	0.351	0.098	0.000	0.000	0.000	0.000	0.000	4.202
13	Ni	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
14	Zn	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

	NOD1	NOD2	NOD3	NCC2	GUT1	P1	NCC3	FN1	FN2	PF1
1	6.037	1.238	2.509	0.255	2.297	0.000	1.947	0.000	0.068	14.932
2	3.637	0.513	1.650	0.101	1.521	0.000	0.712	0.000	0.000	9.211
3	0.000	0.171	0.000	0.000	0.789	0.000	0.000	0.000	0.000	0.088
4	2.094	0.550	0.440	0.203	1.223	5.067	0.426	0.000	0.000	1.366
5	13.603	13.271	12.150	7.461	8.129	2.772	22.272	17.098	5.076	7.822
6	0.561	0.808	0.293	0.292	0.580	0.000	0.367	0.125	0.000	0.790
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.558	0.000	0.000	0.660	0.000	0.474	0.415	0.000	0.000
9	0.898	0.111	0.321	0.000	18.118	0.000	0.122	0.000	0.000	1.417
10	0.192	0.151	5.786	0.000	2.163	0.356	9.058	9.578	4.145	0.000
11	0.440	0.247	0.504	0.374	0.495	14.353	0.174	0.212	0.129	0.078
12	0.135	0.628	0.062	0.061	17.420	0.000	0.800	0.000	0.045	0.070
13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
14	0.000	0.000	0.000	0.000	0.305	0.000	0.000	0.000	0.212	0.000

	PF2	F18	F19	F20	F21	F22	PF4	PF5	PF6	F23
1	3.536	22.976	11.170	3.079	0.864	0.000	1.724	0.663	13.204	2.468
2	1.109	0.450	1.281	1.436	0.494	0.000	0.697	0.394	12.646	1.008
3	0.356	0.000	0.085	0.549	0.074	0.000	0.280	9.733	3.714	0.000
4	1.165	0.194	0.729	1.149	1.975	0.000	0.589	0.000	0.225	0.559
5	11.588	5.792	5.988	11.814	17.123	11.515	12.825	0.750	1.749	5.311
6	1.759	0.298	0.527	0.027	0.276	0.142	1.344	0.000	0.283	0.604
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.723	0.299	0.815	0.000	0.000	0.329	2.633
9	0.143	0.000	0.175	0.241	0.000	0.000	0.093	0.000	0.217	0.247
10	0.000	0.839	0.000	3.889	0.862	7.371	0.000	0.000	0.000	0.000
11	0.403	0.079	0.295	1.512	0.362	0.204	0.421	8.828	3.330	2.006
12	0.107	0.095	0.113	2.019	0.460	0.055	0.163	0.000	0.126	2.452
13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
14	0.000	0.000	0.000	0.191	0.000	0.000	0.000	0.000	0.000	0.000

	F24	F25	P3	P4	C2	C3	P5	P6	NCB2 P7	PF6
1	0.088	0.224	0.066	0.000	7.012	7.124	1.757	0.000	0.062	15.608
2	0.093	0.000	0.269	0.000	6.404	1.625	0.509	0.000	0.082	11.668
3	0.000	0.000	3.331	3.154	0.296	0.000	6.652	0.000	0.000	0.000
4	0.000	0.000	0.000	0.000	3.008	0.801	0.000	7.062	0.104	0.256
5	14.779	55.728	0.722	0.487	19.735	25.026	1.978	0.154	0.665	0.907
6	0.251	0.000	0.000	0.000	1.243	0.406	0.000	0.000	0.000	0.228
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.328	0.000	0.000	0.451	0.000	0.000	0.000	0.000	0.000	1.565
9	0.000	0.000	0.000	0.000	0.000	0.187	0.000	0.000	0.000	0.269
10	5.370	4.167	0.186	0.100	1.921	0.772	0.000	0.000	0.000	0.000
11	0.070	0.116	4.527	4.711	1.241	0.638	6.684	21.642	7.523	0.173
12	0.000	0.000	0.000	0.000	1.163	0.559	0.000	0.000	0.000	0.256
13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
14	0.000	0.129	0.168	0.230	0.000	0.000	0.000	0.229	0.268	0.000

Element	CRUST 1	PF9	F26	PF10	SED2	SED3
Si	0.000	0.185	0.000	43.749	1.932	1.650
Al	0.000	0.000	0.000	37.886	0.977	0.625
Ti	0.000	0.000	0.000	0.000	0.000	0.000
Fe	0.000	2.010	0.164	0.000	0.273	0.233
Ca	38.468	50.855	49.458	0.000	48.153	47.503
Mg	0.894	1.181	0.000	0.000	0.000	0.000
Na	0.000	0.000	0.424	0.000	0.000	0.000
K	0.000	0.000	0.115	0.000	0.137	0.000
P	0.199	0.000	36.098	0.000	35.837	35.136
S	0.000	0.000	0.000	0.000	0.000	0.000
Cl	0.071	0.000	0.120	0.000	0.073	0.092
Zn	0.000	0.000	0.000	0.000	0.000	0.000

	C1	PF11	NCB4C1	NCB4C2P	NCB4C2	NCB4C3	NCB4C4
1	0.289	44.042	0.000	12.122	3.124	59.341	0.000
2	0.000	34.918	0.000	9.984	3.304	10.749	0.140
3	0.000	0.000	0.000	0.000	0.000	0.263	0.000
4	0.000	0.000	0.000	0.939	0.295	1.667	0.000
5	35.678	0.000	0.565	0.194	0.142	0.374	1.181
6	0.000	0.000	0.732	0.000	0.321	0.478	0.582
7	0.000	0.000	0.000	2.404	0.793	1.758	0.000
8	0.000	0.000	0.000	0.221	0.131	3.321	0.000
9	26.441	0.000	0.000	0.000	0.000	0.000	0.000
10	0.241	0.000	0.917	2.560	1.008	0.652	0.550
11	0.130	0.000	0.000	1.019	0.512	0.833	0.053
12	0.000	0.000	0.000	0.000	0.000	0.000	0.135

	NCB4C5	NCB4C6	NCB4C6P	PF12	F27	SED4	SED5
1	0.150	0.000	4.724	44.036	0.954	18.937	10.864
2	0.000	0.000	5.083	38.127	0.724	5.299	6.674
3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4	0.000	0.000	42.253	0.000	0.000	0.592	5.607
5	0.171	0.342	0.000	0.000	50.402	32.193	31.700
6	0.270	0.352	0.000	0.000	0.000	0.000	0.248
7	0.429	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.161	0.557
9	0.000	0.000	0.000	0.000	36.450	24.135	23.821
10	0.530	0.690	94.081	0.000	0.000	0.495	13.565
11	0.540	0.061	0.000	0.000	0.000	0.122	0.000
12	0.000	0.000	0.343	0.000	0.000	0.000	0.000

	C2	PF13	F28	F29	C3	SED6	PF14
1	0.000	43.540	0.000	0.000	0.301	3.133	43.566
2	0.000	38.361	0.000	0.000	0.000	1.281	37.655
3	0.158	0.000	0.000	0.000	0.000	0.000	0.000
4	0.000	0.000	0.000	0.360	0.000	0.384	0.000
5	51.749	0.000	48.736	49.798	50.617	47.782	0.000
6	0.000	0.000	0.000	0.442	0.510	0.000	0.000
7	0.395	0.000	0.557	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000
9	33.298	0.000	35.642	22.357	24.898	35.712	0.000
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000
11	0.000	0.000	0.129	0.000	0.000	0.000	0.000
12	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Best enterosp. data 15/6/88

	PF15	F30E	F31E	F32E	F33E	PF16	F34E
1	44.406	0.000	0.000	0.000	0.000	0.000	0.000
2	37.715	0.000	0.000	0.000	0.000	0.000	0.000
3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4	0.153	0.292	0.188	0.279	0.223	1.544	0.362
5	0.000	51.303	48.551	50.862	49.474	52.716	50.793
6	0.000	0.000	0.000	0.000	0.000	1.927	0.000
7	0.000	0.969	0.409	0.423	0.648	0.000	0.968
8	0.123	0.000	0.000	0.000	0.000	0.000	0.000
9	0.000	38.037	34.665	37.184	35.450	0.800	37.396
10	0.000	0.000	0.466	0.000	0.576	0.000	0.000
11	0.066	0.094	0.123	0.106	0.000	0.000	0.092
12	0.000	0.000	0.000	0.000	0.000	0.000	0.000

	F35E	F36E	F37E	F38E	F39E	C4	SED7
1	0.000	0.000	0.000	0.000	0.000	0.000	17.254
2	0.000	0.000	0.000	0.000	0.000	0.000	9.626
3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4	0.000	0.254	0.262	0.233	0.197	0.324	2.681
5	48.120	51.127	46.881	50.912	50.251	43.071	29.412
6	0.000	0.000	0.000	0.000	0.000	0.345	1.098
7	0.000	1.251	0.000	0.660	0.371	0.411	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.935
9	34.619	37.749	34.341	38.128	35.641	30.717	22.152
10	0.881	0.000	0.408	0.000	0.386	0.000	0.000
11	0.131	0.075	0.142	0.130	0.000	0.171	0.000
12	0.000	0.000	0.000	0.000	0.000	0.000	0.000

	SED8C	SED9D	CRUST2	CRUST3	CRUST4	CRUST5	CRUST6
1	47.815	54.222	0.000	0.000	0.244	0.000	0.000
2	9.842	15.045	0.000	0.000	0.000	0.000	0.000
3	0.160	0.268	0.000	0.000	0.000	0.000	0.000
4	1.385	2.514	0.000	0.383	0.214	0.000	0.000
5	0.113	0.137	51.053	45.850	51.833	19.294	38.027
6	0.587	1.132	1.062	1.004	1.306	0.000	0.000
7	0.000	0.000	0.000	0.000	0.385	0.000	0.000
8	1.250	1.942	0.000	0.000	0.000	0.000	0.000
9	0.000	0.000	1.161	0.509	0.690	14.727	26.763
10	0.369	1.435	0.937	1.071	1.229	1.431	1.271
11	0.093	0.000	0.000	0.000	0.000	0.000	0.000
12	0.000	0.000	0.000	0.000	0.000	0.000	0.000

	Element	PF7	C4	PF8	CRUST7	AV SED10
1	Si	3.0770	0.0000	12.4746	0.000	40.311
2	Al	1.3233	0.0000	8.0470	0.000	20.231
3	Ti	0.1598	0.0000	0.1854	0.000	0.642
4	Fe	0.4144	0.0975	1.8512	0.328	5.700
5	Ca	3.9216	12.4579	2.9959	39.457	0.393
6	Mg	0.2305	0.1442	0.5852	0.231	1.452
7	Mn	0.0000	0.0000	0.0000	0.441	0.000
8	Na	3.5576	0.3710	0.5835	0.177	2.436
9	K	0.7919	0.0000	1.0255	28.762	0.000
10	P	0.9386	7.8557	0.0000	1.467	6.940
11	S	0.7998	0.1030	0.2772	0.000	0.000
12	Cl	1.5988	0.1123	0.1124	0.000	0.000
13	Ni	0.0000	0.0000	0.0000		
14	Zn	0.0000	0.1146	0.0000		

b

Coprolite data

	Tl	mt	mt/Tl	lmt	nt	Tl-nt (T)	mt-nt (m)	T/m	chars
1	15.6	9.6	0.615	10.5	0.0	15.600	9.600	1.625	sp
2	17.2	15.8	0.919	8.7	2.0	15.200	13.800	1.101	sp
3	17.5	18.0	1.029		0.0	17.500	18.000	0.972	sp,
4	20.0	11.6	0.580	10.5	0.0	20.000	11.600	1.724	sp
5	20.5	21.0	1.024	13.7	5.5	15.000	15.500	0.968	t
6	21.2	18.0	0.849		2.5	18.700	15.500	1.206	sp
7	21.6	12.0	0.556	11.3	2.0	19.600	10.000	1.960	sp
8	22.0	14.0	0.636	12.7	2.7	19.300	11.300	1.708	sp
9	22.0	11.2	0.509	15.6	0.0	22.000	11.200	1.964	sp
10	22.5	15.0	0.667	11.3	2.3	20.200	12.700	1.591	n
11	23.0	17.7	0.770	12.0	3.0	20.000	14.700	1.361	n
12	23.3	11.5	0.494	11.9	1.8	21.500	9.700	2.216	n
13	23.4	16.7	0.714	14.0	3.0	20.400	13.700	1.489	n
14	23.6	21.0	0.890	13.6	5.5	18.100	15.500	1.168	sp
15	24.0	21.1	0.879	12.0	3.6	20.400	17.500	1.166	n
16	24.0	16.1	0.671	12.1	2.7	21.300	13.400	1.590	n
17	24.0	20.3	0.846	22.0	4.3	19.700	16.000	1.231	sp
18	24.1	17.3	0.718	12.8	4.6	19.500	12.700	1.535	sp
19	24.2	16.3	0.674	12.1	4.8	19.400	11.500	1.687	sp
20	24.9	13.0	0.522	13.0	2.5	22.400	10.500	2.133	n
21	25.0	23.0	0.920	13.0	6.0	19.000	17.000	1.118	sp
22	26.1	14.0	0.536	16.1	0.0	26.100	14.000	1.864	sp
23	26.6	20.6	0.774	13.4	2.1	24.500	18.500	1.324	n
24	27.0	19.4	0.719	15.1	5.0	22.000	14.400	1.528	sp
25	27.9	22.4	0.803	15.0	2.2	25.700	20.200	1.272	n
26	28.0	12.8	0.457	16.0	2.0	26.000	10.800	2.407	sp
27	28.0	15.5	0.554	16.2	2.0	26.000	13.500	1.926	n
28	28.2	25.2	0.894	15.5	2.4	25.800	22.800	1.132	sp
29	28.2	20.1	0.713	16.2	2.7	25.500	17.400	1.466	n
30	28.4	18.4	0.648	14.2	4.9	23.500	13.500	1.741	n
31	28.7	13.2	0.460	14.4	0.0	28.700	13.200	2.174	sp
32	28.9	12.4	0.429	15.1	0.0	28.900	12.400	2.331	sp
33	29.0	17.5	0.603	15.2	5.9	23.100	11.600	1.991	n
34	29.0	20.6	0.710	15.2	2.6	26.400	18.000	1.467	t
35	29.2	24.0	0.822	18.7	2.0	27.200	22.000	1.236	sp
36	30.3	16.7	0.551	20.5	3.2	27.100	13.500	2.007	n
37	30.5	12.8	0.420	12.0	0.0	30.500	12.800	2.383	sp
38	31.0	20.0	0.645	16.2	6.2	24.800	13.800	1.797	n
39	31.3	20.0	0.639	17.6	3.0	28.300	17.000	1.665	n
40	32.0	18.8	0.588	19.1	2.5	29.500	16.300	1.810	sp
41	32.2	24.7	0.767	20.8	2.8	29.400	21.900	1.342	sp
42	32.6	20.0	0.613	19.2	3.0	29.600	17.000	1.741	sp
43	33.0	20.0	0.606	21.5	0.0	33.000	20.000	1.650	ns
44	33.0	9.4	0.285	26.0	0.0	33.000	9.400	3.511	n
45	33.2	16.5	0.497	22.6	0.0	33.200	16.500	2.012	sp
46	33.4	18.4	0.551	17.1	3.4	30.000	15.000	2.000	sp
47	33.5	13.7	0.409	27.3	0.0	33.500	13.700	2.445	sp
48	34.0	10.7	0.315	21.0	0.0	34.000	10.700	3.178	sp
49	34.1	21.5	0.630	17.7	2.4	31.700	19.100	1.660	sp
50	35.5	22.3	0.628	20.6	3.7	31.800	18.600	1.710	sp
51	35.5	5.0	0.141	30.0	0.0	35.500	5.000	7.100	n
52	36.0	14.0	0.389	20.0	0.0	36.000	14.000	2.571	sp
53	37.6	15.4	0.410	20.0	2.5	35.100	12.900	2.721	n
54	37.8	16.5	0.437	21.0	2.6	35.200	13.900	2.532	n
55	38.4	20.5	0.534	19.3	6.3	32.100	14.200	2.261	sp
56	39.0	24.7	0.633	20.0	2.3	36.700	22.400	1.638	n
57	41.0	26.8	0.654	22.0	0.0	41.000	26.800	1.530	n
58	43.0	16.8	0.391	25.2	4.0	39.000	12.800	3.047	n
59	46.9	13.9	0.296	34.6	0.0	46.900	13.900	3.374	n
60	53.6	15.0	0.280	41.4	0.0	53.600	15.000	3.573	sp